

THE RESSERELLINAE—A NEW SUBFAMILY OF LATE ORDOVICIAN TO EARLY DEVONIAN DALMANELLID BRACHIOPODS

by V. G. WALMSLEY and A. J. BOUCOT

ABSTRACT. A new subfamily Resserellinae of the Dalmanellidae is proposed to include *Resserella* Bancroft, *Fascicostella* Schuchert and Cooper, *Dedzetina* Havlíček, and *Visbyella* Walmsley, Boucot, Harper, and Savage.

It is considered that *Dedzetina* (late Ordovician) gave rise to *Visbyella* (late Llandoveryan to Wenlockian) and *Resserella* (late Llandoveryan to Emsian). *R. sefinensis* sp. nov. (late Llandoveryan, C₁) is the oldest *Resserella* known. Four lineages of *Resserella* are recognized: (1) *R. concavoconvexa* (late Llandoveryan, C₃–C₆, to early Wenlockian) from Anticosti, ?New Brunswick, ?Quebec, ?South Wales, and Estonia; *R. elegantulina* (early Wenlockian), Shropshire; *R. basalis* (Wenlockian) of Gotland and the Welsh Borderland; and *R. waldronensis* (Wenlockian) of Ohio. (2) *R. springfieldensis* (late Llandoveryan, C₄–C₆) of Podolia, (early Wenlockian) of Britain, (Wenlockian) of Ohio; *R. canalis* (Wenlockian and Ludlovian) of Gotland and Britain; *R. elegantula* (Wenlockian) of Gotland; and *R. logansportensis* sp. nov. (Pridolian) of Indiana. (3) *R. brownspontensis* (late Wenlockian) of South Wales and (Ludlovian) of Tennessee; *R. amsdeni* sp. nov. (Ludlovian) of Oklahoma; *R. elegantuloides* (Gedinnian) of Podolia and Nevada; and *R. triangularis* (Emsian) of Rhineland and Kazakhstan. (4) *R. crassicostata* (Ludlovian) of Tennessee and Oklahoma; *R. impeusa* (Siegenian) of Victoria, Australia; and *R. pragensis* (Emsian) of Bohemia. The latter lineage is considered to have given rise in the Gedinnian to *Fascicostella gervillii* (Gedinnian to Eifelian) of Europe and North Africa, *F. undulata* sp. nov. (early Devonian) of Belgium and *F. batonensis* sp. nov. (Siegenian) of New Zealand.

THE genera and species of dalmanellid brachiopods here described have a sufficiently discernible natural affinity to permit their being gathered together into a separate subfamily. The new subfamily Resserellinae is proposed, to encompass the genera *Resserella* Bancroft 1928, *Fascicostella* Schuchert and Cooper 1931, *Dedzetina* Havlíček 1950, and *Visbyella* Walmsley, Boucot, Harper, and Savage, 1968.

This paper attempts to clarify the morphology, taxonomy, stratigraphic distribution, phylogeny, and geographic distribution of these genera and their member species so as to render the group more useful stratigraphically.

During a study made by Walmsley in 1963 at the California Institute of Technology, of dalmanellid material collected by Boucot from many localities in Gotland, Britain, Oklahoma, Tennessee, and Indiana, several species of *Resserella* were recognized including three new ones. Type and figured material was then borrowed from museums in an attempt to describe the remaining *Resserella* species. During a visit to the Senckenberg Museum, Frankfurt in 1965, Walmsley examined Early Devonian dalmanellid material and recognized *Orthis triangularis* Maurer as a resserellid. Maurer's original material was examined at the Hessisches Landesmuseum Darmstadt in 1966. Study of Dalman's material at the Natural History Museum, Stockholm, enabled Walmsley to select the lectotype of *R. basalis*. Boucot provided locality and stratigraphic data for his collected material and general guidance during the laboratory study and in the writing of this paper.

There has been much confusion over some of the species and the genus *Resserella* here assigned to the new subfamily Resserellinae. Since Dalman (1828, p. 117, and pl. II, fig. 6) erected the species *Orthis elegantula*, many dissimilar shells have been assigned

to it. Investigation of material from Gotland has revealed that at least four species of resserellinid brachiopods occur there (*R. elegantula*, *R. canalis*, *R. basalis*, and *V. visbyensis*) and as no types had been selected, some confusion was inevitable. Dalman's figures of *O. elegantula* have proved inadequate and indeed even misleading in that the species is represented as being more elongate than the type material. Material from the Swedish Museum of Natural History, which was collected by Hisinger, is the collection on which Dalman based his species *O. elegantula*. The lectotype SMNH Br. 1202201 has been selected from this collection and is figured here Plate 91, fig. 5.

J. de C. Sowerby (in Murchison 1839, pp. 630 and 640, pl. 13, fig. 12a and pl. 20, fig. 8) erected *Orthis canalis* now known to be based on two distinct species. One, of Ordovician (Caradocian) age, was renamed *Paucicrura sowerbyi* by Cave and Dean (1959, p. 295) and subsequently assigned by Williams (1963, p. 389) to *Howellites* as *H. antiquior* (McCoy). The other of Silurian (Wenlockian to Ludlovian) age, is *Resserella canalis*.

Bancroft (1928, p. 54) erected the genus *Resserella* and cited *O. canalis* J. de C. Sowerby as the type species but without selecting a lectotype. When Schuchert and Cooper (1932 p. 126) selected a lectotype they cited *O. canalis* Sowerby 1839, plate 13, fig. 12a, the Wenlock age shell which is congeneric with *O. elegantula* Dalman. As the latter had been selected by them as the type species of their genus *Parmorthis*, *Parmorthis* became a subjective synonym of *Resserella*. Cooper pointed this out in 1956 (p. 956), and in most subsequent papers, species congeneric with *O. elegantula* have been assigned to *Resserella*. However, in pre-1956 literature this name refers to the Ordovician genus and caution is therefore necessary in interpreting the name *Resserella* in a particular reference.

The fourth resserellinid species from the Gotland material has recently been re-described as the type species *V. visbyensis* (Lindström), of a new genus *Visbyella* (Walmsley, Boucot, Harper, and Savage 1968, p. 306).

In erecting *Fascicostella*, Schuchert and Cooper (1931, p. 246) were aware of its close similarity internally to *Parmorthis* [= *Resserella* of this paper] and Havlíček (1950, p. 33), recognized the resserellinid affinities of *Dedzetina* by making it a subgenus of *Parmorthis*.

In regarding the Dalmanellidae as being better placed in the superfamily Dalmanellacea Schuchert 1913, than in the Enteletacea Waagen 1884, we subscribe to the view of Johnson and Talent (1967, pp. 142–143) already adopted by Walmsley (in press).

SYSTEMATIC PALAEONTOLOGY

Suborder DALMANELLOIDEA

Superfamily DALMANELLACEA Schuchert 1913 [= RHIPIDOMELLACEA Alichova 1960]

Family DALMANELLIDAE Schuchert 1913

Subfamily RESSERELLINAE nov.

Diagnosis. Aseptate or septate plano-convex, slightly concavo-convex or ventribiconvex Dalmanellidae, commonly shield-shaped, with a prominent beak on the deep pedicle valve. Commonly having a distinctive asymmetrical pattern of bifurcating costellae in the medial region of the brachial valve. Costellae may be evenly or unevenly ramicos-tellate or fascicostellate. Brachioophores widely divergent, and cardinal process bilobed

or trilobed. Ventral muscle field small, cordate. Teeth and sockets commonly crenulated and associated with accessory articulation.

Comparison. The Resserellinae are generally distinguished from other members of the Dalmanellidae (the Dalmanellinae, Isorthinae, and Cortezorthinae—see Walmsley, Boucot, and Harper 1969, text-fig. 4), by the extreme inequality of convexity of the valves, the pedicle valve always being very much more convex than the brachial valve, which may be slightly convex, flat, or even slightly concave. Associated with the deep convexity of the pedicle valve is the commonly prominent, strongly curved beak which in some cases overhangs the hinge line. The shield-shaped outline is fairly characteristic though not confined to this subfamily (see Walmsley 1965, p. 474), and the branching pattern of the medial costellae in the brachial valve is usually distinctive. The brachial valve muscle field and cardinalia, with the commonly crenulated sockets and widely divergent brachiophores are distinct from those of other dalmanellids as are the generally ponderous teeth, often with crural fossettes. The major variations within the subfamily, recognized in its member genera, concern the bundling of the costellae, the nature of the cardinal process, the attitude of the cardinal area in the brachial valve, and presence or absence of an apical plate or pedicle callist.

Genera assigned to Resserellinae

Resserella Bancroft 1928 [= *Parmorthis* Schuchert and Cooper 1931]

Fascicostella Schuchert and Cooper 1931

Dedzetina Havlíček 1950

Visbyella Walmsley, Boucot, Harper, and Savage 1968

Morphological features of the Resserellinae. Schuchert and Cooper (1932, p. 129) have already commented on the distinctive morphology of *Resserella* [*Parmorthis*] and especially the strength of the articulatory parts. Not only are the teeth and sockets usually large and crenulated (see our Pl. 95, fig. 8a, and Pl. 96, fig. 4d), but the articulation is further secured by the fitting of peg-like brachiophore processes (see Pl. 93, fig. 5a, and Pl. 96, fig. 4d, g) into usually deep crural fossettes, excavated in the antero-medial faces of the teeth (see Pl. 95, fig. 8c and Pl. 99, fig. 6a). Commonly the dorsal surfaces of the hinge teeth also bear accessory dental sockets (see Pl. 95, fig. 8a and Pl. 97, fig. 3a) which engage small accessory teeth (outer socket ridges) formed along the posterior edges of the sockets in the brachial valve. Crural fossettes and accessory teeth and sockets are also present in *Visbyella* and *Fascicostella*.

An apical plate is present in *Visbyella* (Walmsley, Boucot, Harper, and Savage 1968, p. 307), and a pedicle callist is present in both *Dedzetina* and *Resserella*. The vascula media are divergent in *Dedzetina* but sub-parallel in *Resserella*, *Visbyella*, and *Fascicostella*. The dorsal interarea is hypercline in *Dedzetina* and *Visbyella* but anacline in *Resserella* and *Fascicostella*.

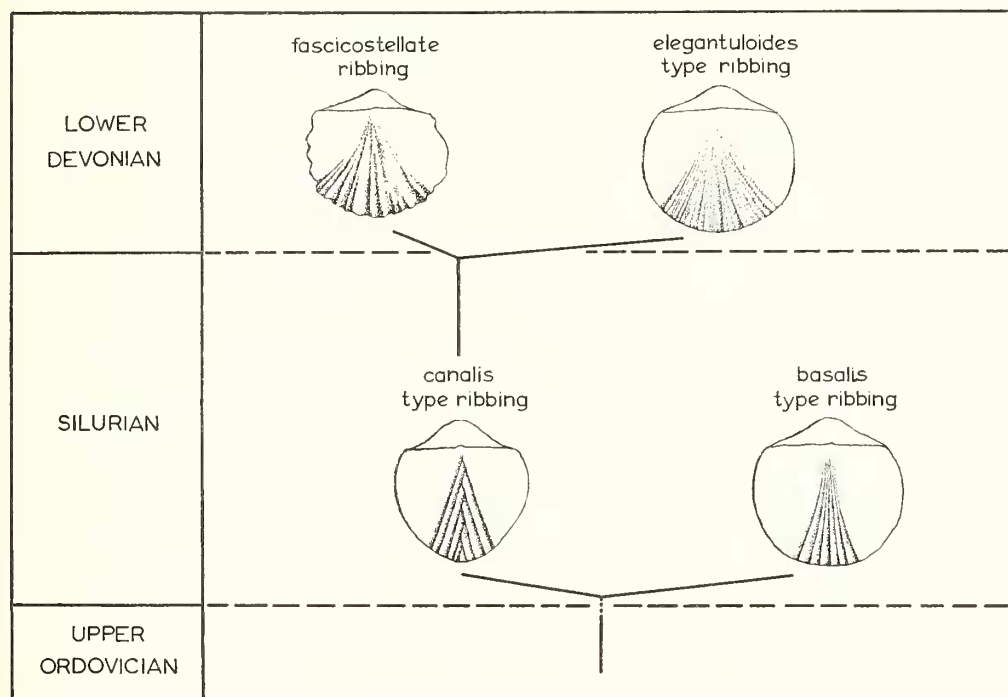
The relative size, position, and orientation of the articulatory features help to characterize resserellid species. However, the major distinguishing characters of resserellid species are the outline, relative convexity of the valves (especially the brachial valve), the development of incurved beaks and especially the ribbing pattern.

The distinctive nature of the resserellid pattern of asymmetrical bifurcation of the medial costellae in the brachial valve was pointed out and illustrated by Walmsley (1965,

TABLE 1. Diagnostic characters of resserellinid genera

	<i>Outline</i>	<i>Profile of brachial valve</i>	<i>Ribbing</i>	<i>Dorsal interarea</i>	<i>Cardinal process</i>	<i>Dorsal median ridge</i>	<i>Dorsal adductor scars</i>	<i>Brachioophores</i>	<i>Apical plate</i>	<i>Pedicle callist</i>	<i>Vascula media</i>
<i>Dedzertina</i>	Transversely elliptical	Convex	Multicostellate with even, angular ribs with wide interspaces	Hypercline	Bilobed	Low	Anterior pair larger than posterior pair	Very widely divergent	Absent	Present	Divergent
<i>Resserella</i>	Sub-circular to elongate shield-shape	Concave, plane, or very slightly convex	Asymmetrically branched pattern of even or semi-fascicostellate ribs	Anacline	Bilobed	Low	Anterior pair usually smaller than posterior pair	Widely divergent	Absent	Present	Sub-parallel
<i>Vishyella</i>	Elongate shield-shape to semi-circular	Concave, plane, or slightly convex	Asymmetrically branched pattern of even ribs	Hypercline	Trilobed exverted	May be separate anteriorly	May be smaller than, equal to, or larger than posterior pair	Divergent	Present	Absent	Sub-parallel
<i>Fascicostella</i>	Sub-circular to sub-quadrate	Concave or plane	Asymmetrically branched pattern. Strongly fascicostellate	Anacline	Bilobed	Low	Anterior pair smaller than posterior pair	Very widely divergent	Absent?	?	Sub-parallel

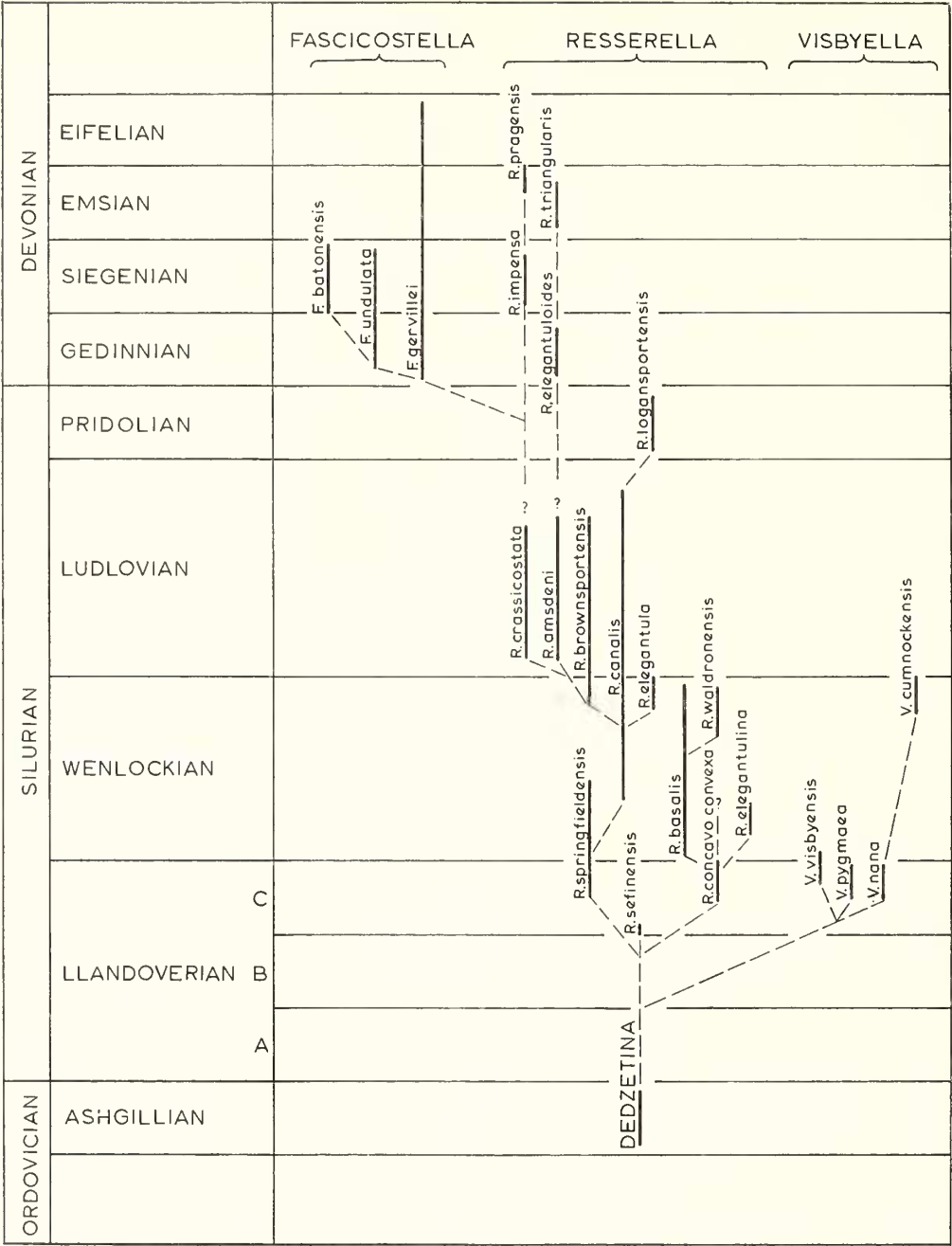
pp. 456–457 and text-fig. 1). It may be clearly seen in a number of the shells figured in the present paper (see Pl. 96, fig. 2*d*) and in the species of *Visbyella* (see Walmsley, Boucot, Harper, and Savage 1968, pl. 60, fig. 4*a*). Even when the preservation does not permit the tracing of the primary costellae, the pattern is usually evident as a medial triangular sector often of finer costellae, distinguishable from lateral areas in which the costellae curve. In detail, the pattern developed in these medial sectors and the density, number, and degree of uniformity of the costellae provide useful diagnostic features. In a general way (text-fig. 1) it is possible to pick out four main types of ribbing pattern in *Resserella*.



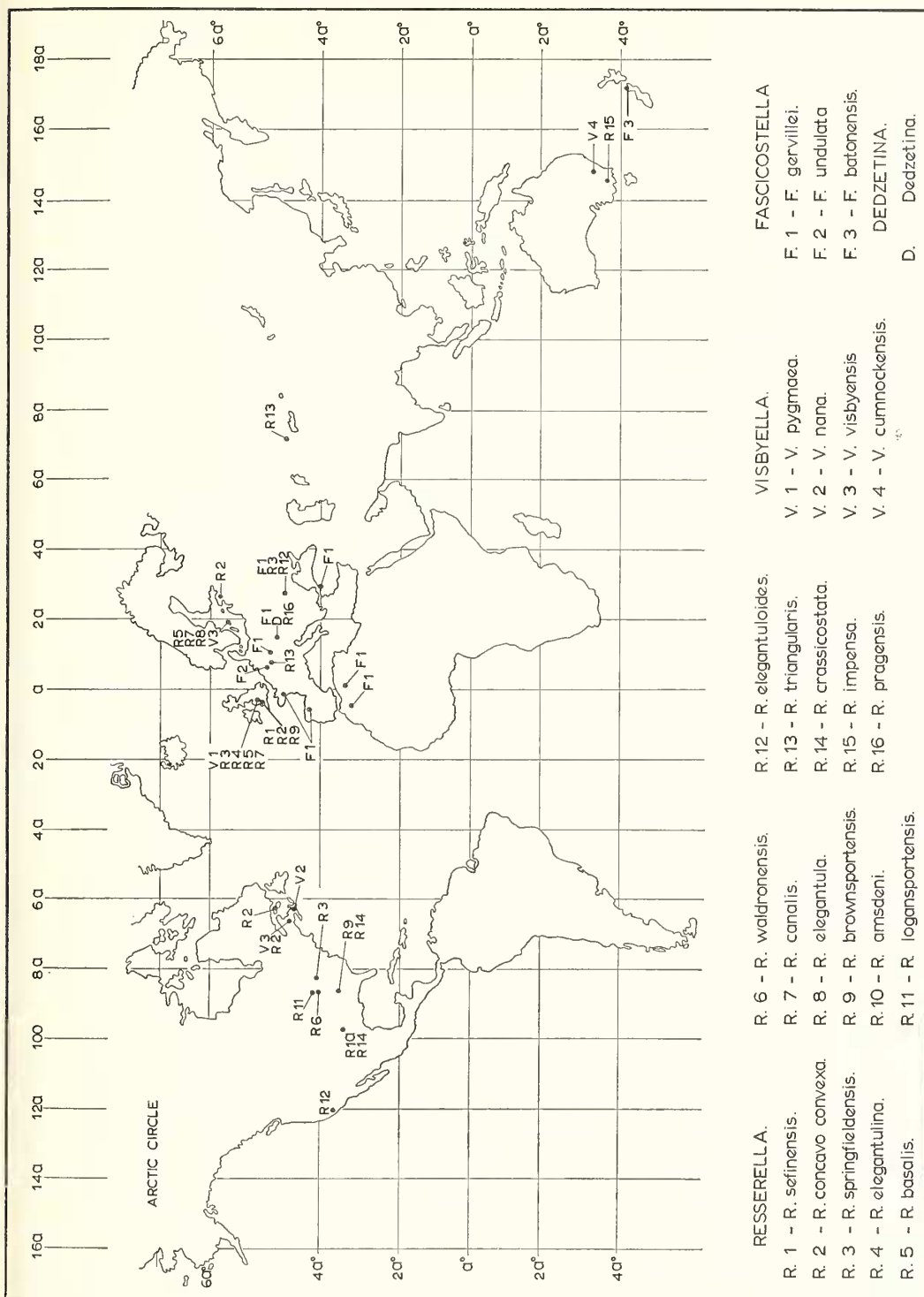
TEXT-FIG. 1. Showing three different styles of ribbing in the medial panel of the brachial valve of *Resserella* species and the fascicostellate pattern as seen in *Fascicostella*.

Fascicostella is strongly fascicostellate. *Dedzetina*, the probable ancestral genus has not clearly developed the asymmetrical pattern.

In *Resserella*, what may be referred to as the *canalis* type of ribbing, is even, medium coarse, with a median depression on the pedicle valve which is narrow, has finer costellae and is almost parallel-sided (see descriptions of species for details). On the brachial valve, the medial sector of slightly finer costellae is acutely triangular (see *R. springfeldensis*, *R. canalis*, *R. elegantula*, *R. logansportensis*, and *R. brownsportensis*). The *basalis* type of ribbing is also even and medium coarse, but the medial costellae in the brachial valve branch relatively early and result in more nearly parallel medial costellae and a more parallel sided medial sector (see *R. basalis*, *R. waldronensis*, *R. elegantulina*, and possibly *R. concavoconvexa*).



TEXT-FIG. 2. Time-stratigraphic ranges of resserellinid species and suggested phylogeny of species and genera.



TEXT-FIG. 3. The geographic distribution of resserellinid species and genera.

The *elegantuloides* type is uneven, tending to be semifascicostellate and possibly originated in *R. brownsportensis* (see *R. amsdeni*, *R. elegantuloides*, and *R. triangularis*). The *pragensis* type is a coarser, uneven, and somewhat fascicostellate pattern developed probably from *R. crassicostata* (see *R. impensa* and *R. pragensis*).

Distribution of resserellinids in time and space. Until all the resserellinid species have been recognized and recorded both stratigraphically and geographically, any attempt to plot resserellinid distribution may appear to be premature and incomplete. Nevertheless, the material described in this paper was derived from many parts of the world and even tentative suggestions may prove helpful in guiding further searches.

The time-stratigraphic ranges of resserellinid species and the suggested phylogeny of species and genera are illustrated in text-fig. 2. This is based on morphological comparisons and relative age (so far as correlations are reliable). The known geographic distribution of resserellinids is summarized in text-fig. 3, the details of localities are given under each species. A study of these two text-figures together suggests possible migratory routes and indicates areas from which further data may be forthcoming.

Genus RESSERELLA Bancroft 1928

Type species. *Orthis canalis* J. de C. Sowerby in Murchison 1839, p. 630, plate 13, fig. 12a.

Diagnosis. Plano-convex to ventribiconvex shield-shaped resserellinids having a bilobed cardinal process, an anacline dorsal interarea and an even or only semi-fascicostellate ornament commonly with an asymmetrical pattern of bifurcating costellae in the medial region of the brachial valve. Lacking a dorsal median septum and an apical plate.

Species assigned to Resserella

<i>Orthis elegantula</i>	Dalman 1828
<i>Orthis basalis</i>	Dalman 1828
<i>Orthis canalis</i>	J. de C. Sowerby 1839
<i>Orthis elegantulina</i>	Davidson 1881
<i>Orthis triangularis</i>	Maurer 1889
<i>Dalmanella springfieldensis</i>	Foerste 1917
<i>Dalmanella waldronensis</i>	Foerste 1917
<i>Dalmanella concavoconvexa</i>	Twenhofel 1927
<i>Dalmanella elegantuloides</i>	Kozłowski 1929
<i>Parmorthis crassicostata</i>	Schuchert and Cooper 1932
<i>Parmorthis brownsportensis</i>	Amsden 1949
<i>Parmorthis pragensis</i>	Havlíček 1956
<i>Resserella impensa</i>	Philip 1960
<i>Resserella amsdeni</i>	sp. nov.
<i>Resserella logansportensis</i>	sp. nov.
<i>Resserella sefinensis</i>	sp. nov.

Species rejected from Resserella. *Orthis (Dalmanella) elegantula* Dalman var. nov. *drummockensis*, Reed 1917, p. 850, pl. IX, figs. 11–15; *Dalmanella elegantula* mut. *primitiva* McLearn 1924, p. 53, pl. 3, fig. 7 [this is *D. primitiva* (Harper in correspondence)]; *D. elegantula* mut. *transversaria* McLearn 1924, p. 54, pl. 3, figs. 8, 9 [this is *Salopina submedia* (Harper in correspondence)]; *R. canalis* (Sowerby) Bancroft 1928, p. 54; *R. paracyclica* Bancroft 1928, p. 56, pl. 1, figs. 6–9; *R. cyclica* Bancroft 1928, p. 56, pl. 1, fig. 10; *R. canalis* (Sowerby) Bancroft 1929, pp. 36–38; ? *R. canalis* (Sowerby) Schuchert and Cooper 1932, p. 126, pl. 17, figs. 14–16; *R. [Orthis] media* (Shaler), Schuchert and Cooper 1932, p. 129; (*O. media* Shaler was referred with doubt to *Parmorthis* by Schuchert and Cooper; it is here rejected from *Resserella* because its circular outline, fairly convex brachial valve, symmetrical costellae bifurcation, and muscle fields are not resserellid in character); *R. visbyensis* Lindström, Schuchert and Cooper 1932, p. 129; *R. canalis* (J. de C. Sowerby) Whittington 1938a, p. 51, pl. 6, figs. 8–12; *R. cruralis*, Whittington 1938b, p. 247, pl. X, figs. 8–11, *R. canalis* (Sowerby), Bancroft 1945, pp. 193, 195, and 203. *R. (Howellites) intermedia*, Bancroft 1945, p. 205, pl. 27, figs. 1–4, pl. 28, figs. 5–6; *R. (Howellites)*

striata Bancroft 1945, p. 204, pl. 26, figs. 2–10, pl. 27, figs. 13 and 15, pl. 28, figs. 1–3; *R. (Howellites) ultima* Bancroft 1945, p. 209, pl. 27, figs. 10–12, pl. 28, figs. 9–10; *Parmorthis vandiementi* Gill 1948, p. 65, pl. 8, fig. 30 (= *Dalejina*, see Boucot, Johnson, and Walmsley 1965, p. 337); *R. immatura* Williams 1949, p. 165, pl. 8, figs. 1–4; *R. immatura* var. *plana* Williams 1949, p. 167, pl. 8, figs. 5–6; *R. corpulenta* (Sardeson), Wang 1949, p. 37, pl. 3A, figs. 1–9; *R. corpulenta circularis* Wang 1949, p. 38, pl. 3B, figs. 1–8; *Parmorthis (Dedzetina) macrostomoides* Havlíček 1950, p. 34, pl. V, figs. 1–3, 5–7, *P. (Dedzetina) honorata* (Barrande), Havlíček 1950, p. 34, pl. XI, fig. 9, *P. aff. allani* (Shirley), Gill 1950, p. 253, pl. 1, fig. 24 (Shirley's Baton River species *allani* is an isorthis). *R. (Howellites) altera* (Barrande), Havlíček 1950, p. 30, pl. VI, figs. 1, 2, 6, 11, 13, pl. XIII, fig. 1; *P. visbyensis* var. *pygmaea* Whittard and Barker 1950, pp. 575–576, pl. VIII, figs. 9–15; *R. llandoveryana* Williams 1951, p. 96, pl. IV, figs. 7–10; *R. (Howellites) sp.* Whittington and Williams 1955, p. 408, pl. 38, figs. 31–35; *P. crassa* (Lindström) Nikiforova 1954, p. 50, pl. II, figs. 7–11 (= an isorthis); *R. altaica* Kul'kov 1963, p. 15, pl. 1, fig. 2; *R. visbyensis* (Lindström) Rubel 1963, p. 137; *R. cf. visbyensis* (Lindström) Boucot, Johnson, Harper, and Walmsley 1966, p. 14, pl. III, figs. 18–20.

Species requiring further study before assignment. *Orthis dorsoplana* Frech 1888, p. 34, pl. III, figs. 5a–c; *Orthis lodanensis* Frech 1888, p. 32, pl. III, fig. 4; *Dahmanella postelegantula* Weller 1903, p. 232, pl. XX, figs. 21–24; *D. eugeniensis* Williams 1919, p. 118, pl. VII, figs. 1–6; *D. eugeniensis* var. *palaeoelegantula* Williams, 1919, p. 118, pl. VII, figs. 7–8; *D. (Fascicostella?) clarionda* Le Maitre 1944, pp. 25–27, pl. VI, figs. 13–17; *Parmorthis crassa* Borisyak 1955 (non Lindström 1861), p. 18, pl. 1, fig. 2; *P. alata* Borisyak 1955, p. 19, pl. 1, fig. 3; *Parmorthis* sp. Castellaro 1959, p. 42, pl. 1, figs. 18–21; *P. balaensis* Kaplun 1961, pp. 66–67, pl. VII, figs. 1–4; *Resserella* aff. *elegantuloides* (Kozłowski) Kul'kov 1963, p. 14, pl. 1, fig. 1.

Origin of Resserella. The oldest undoubted *Resserella* species described are *R. springfieldensis* (Kataigorod Formation, Podolia, late Llandoveryan, C₄–C₆) and *R. concavoconvexa* (Jupiter Formation, Anticosti Is., late Llandoveryan C₃–C₆).

The oldest *Visbyella* species is *V. pygmaea* (late Llandoveryan C₃ Britain) (Walmsley, Boucot, Harper, and Savage 1968, p. 310).

One of the main differences between *Resserella* and *Visbyella* is the dorsal interarea which in typical *Resserella* is anacline and in *Visbyella* is hypercline. It seems significant that one of the earliest species of *Resserella*, *R. concavoconvexa*, has a dorsal interarea which is intermediate in position, i.e. is catacline (see Twenhofel 1928, p. 179, and pl. XVI, fig. 3). This is also clear from our own Plate 91, fig. 6a. A comparison of *R. concavoconvexa* (Pl. 91, fig. 6) and *V. pygmaea* (Walmsley, Boucot, Harper, and Savage 1968, pl. 61, fig. 1) shows a close general similarity and in view of their similar earliest appearances in middle late Llandoveryan it seems likely that they shared a common origin.

In beds older than late Llandoveryan C₃, no typical *Resserella* or *Visbyella* have yet been recognized. However, in a collection made by Boucot from C₁ beds of the Llandovery area, a new species here assigned to *Resserella* and described as *R. sefinensis*, has a brachial valve interior which is in general resserellid but the exterior of the brachial valve has ribbing which is coarser and does not develop the resserellid asymmetrical pattern in the medial area. This species could be regarded as a form transitional from *Dedzetina* to *Resserella* or as a primitive *Resserella*.

Williams (1951, p. 94) pointed out that no true representatives of *Parmorthis* [= *Resserella* of this paper] had been collected from beds older than Late Llandoveryan (C₁). 'Parmorthis'-like shells collected from the middle, and early late Llandoveryan were considered by Williams to have some morphological features not typically 'parmorthid'. It is possible that the species not described by him but listed (Williams 1951, p. 129) as *Parmorthis* sp. from C₁, is the species here described as *R. sefinensis*. It seems clear that the transition from some earlier form to *Resserella* and possibly *Visbyella* was taking place at about C₁ Llandoveryan time.

Dedzetina was erected by Havlíček (1950 p. 103) as a subgenus of *Parmorthis*, of Late

TABLE 2. Diagnostic characters of species of *Resserella*

	Profile of Brachial valve	Beak of pedicle valve	Outline	Ribbing	
<i>R. amsdeni</i>	Plano-convex	Not overhanging hinge line, high interarea	Transverse	Fine (80 per 9 mm), semi-fascicostellate	Raised median area in dorsal sulcus, median depression along ventral arch
<i>R. basalis</i>	Plano-convex	Not overhanging hinge line, widely separated from beak of brachial valve	Triangular	Medium coarse (45 per 9 mm) median costellae sub-parallel	Teeth elongate, dental lamellae advanced and sub-parallel
<i>R. brownsportensis</i>	Plano-convex	Overhangs hinge line	Elongate- sub-circular	Medium coarse (60 per 9 mm) but fine in wide medial panel	Teeth and crural fossettes, small
<i>R. canalis</i>	Plano-concave	Overhanging hinge line	Elongate	Even medium coarse (60 per 9 mm) medial panel narrow	Teeth, wide, project across commissural plane. Dental lamellae recessive
<i>R. concavoconvexa</i>	Resupinate	Overhangs hinge line widely separated from beak of brachial valve	Transverse	Even, fine	Dorsal interarea catacline
<i>R. crassicostata</i>	Plane	Not overhanging hinge line	Transverse- sub-circular	Even, very coarse (35 per 9 mm) with smooth medial areas	Most coarsely ribbed species
<i>R. elegantula</i>	Convex	Incurved, may overhang hinge line	Transverse	Even, medium coarse (60 per 9 mm)	Teeth wide, massive, heavily crenulated
<i>R. elegantulina</i>	Convex	Overhangs hinge line	Sub-circular	Even, coarse	Small species, brachiophores, thick, stubby
<i>R. elegantuloides</i>	Convex	Not overhanging, high interarea, widely separated from beak of brachial valve	Sub-circular	Uneven, semi- fascicostellate, very fine (100 per 9 mm) with intercalated strong costae	
<i>R. impensa</i>	Plane	Overhangs hinge line	Sub-circular	Uneven, semi- fascicostellate, coarse	Brachiopores, long, very widely divergent
<i>R. logansportensis</i>	Plano-convex	Overhangs hinge line	Elongate	Even, medium coarse (50 per 9 mm)	Teeth long and narrow, dental lamellae erect, sub-parallel and advanced. Raised median ridge in pedicle valve
<i>R. pragensis</i>	?	?	Sub-circular	Uneven, semi- fascicostellate, coarse	Strong dorsal median ridge fused posteriorly with bases of widely divergent brachiophores
<i>R. sefinensis</i>	Plane	?	Sub-circular	Even, coarse	Dorsal muscle field not impressed or elevated
<i>R. springfieldensis</i>	Plane-faintly convex	?	Elongate	Even, coarse, medial panel wide	Dental lamellae, thick and long, long dorsal median ridge
<i>R. triangularis</i>	Plane	Not incurved	Sub-circular to shield-shaped	Even, medium fine (65-70 per 9 mm)	Large species with long dorsal median ridge and thick long brachiophores. Teeth large, dental lamellae short
<i>R. waldronensis</i>	Plano-convex	Small, well separated from beak of brachial valve	Sub-circular- triangular	Even, medium coarse (60 per 9 mm) medial costellae sub-parallel	

Ordovician (Ashgillian) age. In many characters *Dedzetina* is clearly related to *Resserella* [*Parmorthis*] but the outline is transversely elliptical, the ribbing is relatively coarse and symmetrical and the dorsal interarea is hypercline. It is most unfortunate that the dorsal interarea of *R. sefinensis* is not clear in our material (it appears to be hypercline) but in its ribbing it shows affinity with *Dedzetina macrostomoides*, the type species of *Dedzetina*, (see Havlíček's pl. V, fig. 2, our Pl. 91, figs. 3a, b, and compare our Pl. 92, fig. 7b). *R. sefinensis* (C₁) appears to have given rise to *R. springfieldensis* (C₃-C₅)

TABLE 3. Key to *Resserella* species

I. Ribbing even	A With triangular panel of divergent fine costellae in median sector of brachial valve	
	B With sub-parallel median costellae in median sector of brachial valve	
	C Lacking fine costellae in median sector	
II. Ribbing uneven (semi-fascicostellate)	D With fine costellae	
	E With coarse costellae	
A. Outline transverse		<i>R. elegantula</i>
Outline elongate	Dental lamellae short and divergent	Median depression of pedicle valve narrow (2 fine costellae) <i>R. canalis</i>
		Median depression of pedicle valve broad, (4-5 fine costellae) <i>R. brownsportensis</i>
	Dental lamellae long and subparallel	Raised median ridge in pedicle valve <i>R. logansportensis</i>
		No median ridge in pedicle valve <i>R. springfieldensis</i>
B. Beak of pedicle valve overhangs hinge line	Dorsal interarea cataline	<i>R. concavoconvexa</i>
	Brachial valve resupinate	
	Dorsal interarea anacline	<i>R. elegantulina</i>
	Brachial valve convex	
Beak of pedicle valve not overhanging hingeline	Beaks widely separated	<i>R. basalis</i>
	Beaks narrowly separated	<i>R. waldronensis</i>
C.		<i>R. sefinensis</i>
D. With raised median area in brachial valve sulcus and wide median depression along pedicle valve		<i>R. amsdeni</i>
Without ditto	Ventribiconvex	<i>R. elegantuloides</i>
	Large and plano-convex	<i>R. triangularis</i>
E. Short brachiophores	Very coarse ribbing with narrow medial panels of fine costellae	<i>R. crassicostata</i>
	Medium coarse semi-fascicostellate ribbing	<i>R. impensa</i>
Long, very divergent brachiophores		<i>R. pragensis</i>

and possibly to *R. concavoconvexa* (C₃-C₆) and itself to have been derived from *Dedzertina* or some intermediate form of early or middle Llandoveryan age. *R. concavoconvexa* and *V. pygmaea* may have had their origins in some as yet undescribed form transitional between them and *R. sefinensis*.

Four lineages may be distinguished in *Resserella*, the *concavoconvexa*-*basalis*, the *springfieldensis*-*canalis*, the *brownsportensis*-*triangularis*, and the *crassicostata*-*pragensis* lineages. The genus *Visbyella* seems to be most closely related to the first of these and *Fascicostella* to the last of them.

Resserella canalis (J. de C. Sowerby)

Plate 97, figs. 1, 4-7; Plate 98, figs. 1-2; Plate 100, fig. 4

1839 *Orthis canalis*, J. de C. Sowerby in Murchison, pp. 630 and 640, pl. 13, figs. 12a, non pl. 20, fig. 8.

- 1847 *Orthis elegantula* Dalman; Davidson, p. 62, pl. 13, figs. 9–11, *non* Dalman 1828.
1848 *Orthis elegantula* Dalman; Davidson, p. 321, pl. 3, fig. 23, *non* Dalman 1828.
1869 *Orthis elegantula* Dalman; Davidson, p. 211, *pars.* pl. 27, figs. 1–8, ? fig. 9, p. 205, figs. 1–2, *non* Dalman 1828.
non 1928 *Resserella canalis* (J. de C. Sowerby); Bancroft, p. 54.
non 1932 *Resserella canalis* (J. de C. Sowerby); Schuchert and Cooper, pl. 17, figs. 14–16.

Diagnosis. Elongate *Resserella* with sub-parallel lateral margins and rounded anterior margin. Brachial valve plane to slightly concave. Costellae even, medium coarse, with narrow medial panel of finer costellae along pedicle valve. Teeth, project across the commissural plane and bear crural fossettes and accessory sockets.

Comparison. *R. canalis* may be distinguished from *R. elegantula* by its more elongate outline (see Pl. 97, figs. 1a and 2a), its much flatter or even concave brachial valve, its smaller teeth and sockets, smaller brachiophores and absence of fulcral plates. From *R. springfieldensis* it may be distinguished by its much narrower medial panel of finer costellae along the pedicle valve. It differs from *R. basalis* in its less triangular outline and more incurved pedicle valve beak, and from *R. brownsportensis* by its finer costellae and narrower medial panel of finer costellae along the pedicle valve.

Description. Exterior. Plano-convex to slightly concavo-convex, convexity decreasing anteriorly. Brachial valve with shallow median sulcus widening anteriorly. Outline elongately elliptical to shield-shaped. Length slightly greater than width and twice the thickness. Hinge line straight, three-quarters greatest width which is near mid-length. Cardinal angles slightly rounded, anterior and lateral commissures crenulate and slightly flexed. A faint, narrow, flattened or depressed area marks the mid-line. Pedicle valve projects one-fifth total length posterior to hinge line with strongly incurved beak overhanging brachial valve. Interarea anacline in brachial valve, twice as long and strongly curved in pedicle valve, lateral margins sharp. Delthyrium open, triangular, enclosing about 65°. Notothyrium open, but filled with protruding myophore which extends into delthyrium. Costellae relatively coarse, 2.5 per mm at 5 mm length, 60 on a 9 mm wide shell.

Interior of pedicle valve. A broad, flat, barely elevated median area extending to mid-length, separates very faint muscle impressions limited to delthyrial cavity, anterior limit of which on larger shells is marked by a faint rim. Thick dental lamellae meet steep walls of delthyrial cavity at about half their height, bound deep lateral cavities and support small triangular teeth. Teeth, wider than long, bear distinct laterally directed accessory sockets and deep crural fossettes. In larger shells, teeth project beyond dental lamellae. All these features confined to posterior one-third of shell length. Anterior crenulations of shell margin, strong, rounded, and separated by equally wide interspaces.

Interior of brachial valve. Adductor muscle field, confined to median third of posterior half of valve, slightly elevated with raised margins. Margins merge into brachiophore bases and anteriorly curve into midline. Median ridge low, rounded, one-third width of muscle field, narrows between anterior pair of muscle impressions. Faint, oblique antero-lateral ridges separate smaller anterior impressions from posterior pair. Brachiophores diverging anteriorly about 70°, are curved plates, thickened distally and inclined laterally to merge with socket pads which support wide, triangular, crenulated sockets. Cardinal process with broad, grooved shaft and crenulated myophore.

Type specimen. The original of pl. 13, fig. 12a of J. de C. Sowerby in Murchison's *The Silurian System*, is specimen no. GSM 51550, of the Geological Survey Museum (Institute of Geological Sciences), London. It is here designated the lectotype and refigured (Pl. 100, figs. 4a-e).

Distribution. *R. canalis* occurs in the Wenlockian and Ludlovian of the Welsh Borderland and Gotland. Dr. M. G. Bassett (in prep.) provides details of the localities.

He reports that *R. canalis* is fairly common in the Wenlock Shale and Wenlock Limestone of the Welsh Borderland, especially common in the upper Wenlock Shale and Wenlock Limestone of Dudley, and Walsall and occurs in the late Wenlockian mudstones of Pen-y-lan, Cardiff but is unknown from South Central Wales or Pembrokeshire.

R. canalis occurs in material collected by Boucot from the following Gotland localities: canal bank on main road 2 km west and slightly to the south of Klinte Church; uppermost Slite Marl (Wenlockian); quarry of cement plant in Slite, Slite Marl (Wenlockian); just north-east of the main road 2 km north of Grötlingbo church, Eke Marl (Ludlovian).

Remarks. There are few determinations given as *R. canalis* in the literature of the Wenlockian and Ludlovian but many references to *Resserella* [= *Parmorthis*] *elegantula*. It seems most likely that since both species occur in Gotland, although the presence of *R. canalis* there has not hitherto been recognized, there have been many misidentifications. *R. elegantula* is at present known only from the Mulde Marl of Gotland. All references to *R. elegantula* occurring elsewhere should, therefore, be treated with caution.

Resserella elegantula (Dalman)

Plate 91, figs. 5a-d, Plate 95, figs. 8a-c, 9 a-e; Plate 96, figs. 1a-e, 2a-e, 3a-e, 4a-h; Plate 97, figs. 2a, b, 3a, b

- 1828 *Orthis elegantula* Dalman, p. 117, pl. II, figs. 6a-e.
- non 1847 *Orthis elegantula* Dalman; Davidson, p. 62, pl. 13, figs. 9-11.
- non 1848 *Orthis elegantula* Dalman; Davidson, p. 321, pl. 3, fig. 23.
- non 1869 *Orthis elegantula* Dalman; Davidson, p. 211 *pars* pl. 27, figs. 1-8, ? fig. 9, p. 205, figs. 1-2.
- 1932 *Parmorthis elegantula* (Dalman); Schuchert and Cooper, p. 128, pl. 21, figs. 2, 3, 9, 10, 13, 14, 16, 29.

Diagnosis. A transversely shield-shaped (length only slightly greater than width) *Resserella*, having a convex brachial valve (half as deep as the pedicle valve). Beak of pedicle valve strongly incurved, sometimes overhanging the brachial valve. Teeth, massive with curved crenulated faces.

Comparison. *R. elegantula* is distinctive in its combination of transverse outline and convex brachial valve.

Description. *Exterior.* Ventribiconvex with brachial valve half as deep as pedicle valve, convexity decreasing antero-laterally. Brachial valve with narrow posterior median sulcus, widening and fading anteriorly. Outline transversely shield-shaped to sub-circular, slightly rounded cardinal angles, length slightly greater than width, and one and a half times thickness. Hinge line straight, three-quarters of maximum width, which is at mid-length. Pedicle valve outline triangular posterior to hinge line. Beaks close, separated by a distance of one-thirteenth maximum length. Anterior commissure faintly

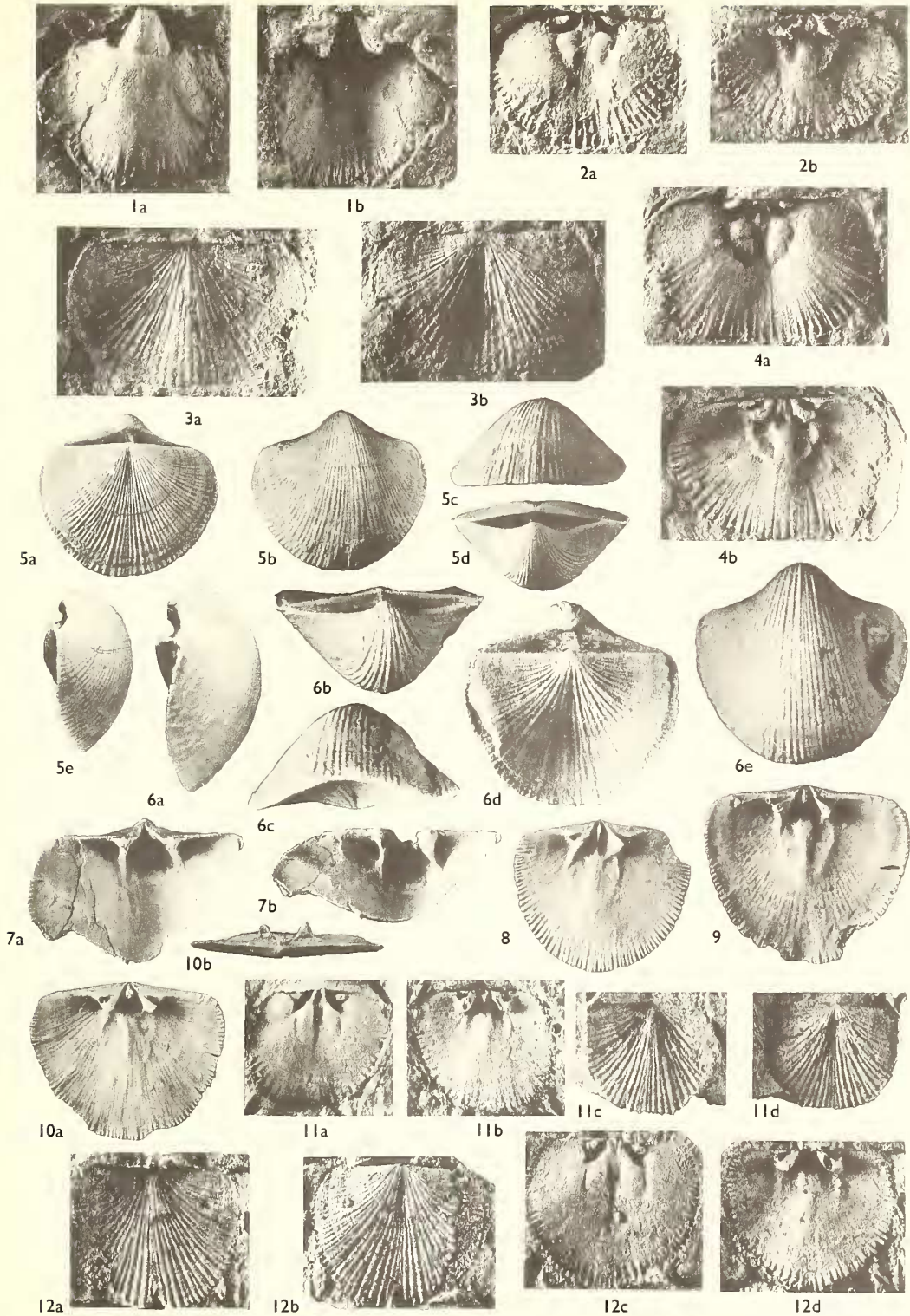
unisulcate and crenulate, lateral commissure crenulate and straight, crenulations may fade laterally. Wide and short interareas, half as long in brachial valve as pedicle valve, growth lines parallel to hinge line; pedicle valve interarea strongly concave dorsally, apsacline, with sharp margins; brachial valve interarea plane, anacline. Open triangular delthyrium, enclosing about 40° , triangular notothyrium, enclosing about 80° , open but filled with protruding cardinal process. Costellae fine, rounded, 4 per mm at 5 mm length, 60 on 9 mm wide brachial valve; median costellae finer and asymmetrically branched (Pl. 96, fig. 2d). Median costellae of pedicle valve finer in a narrow depression.

Interior of pedicle valve. Muscle field faintly impressed, confined to delthyrial cavity, anterior limit of which is marked by a slight step at about one-third length. Thick, short dental lamellae support massive teeth, lateral cavities deep. Teeth triangular in plan and cross-section and bluntly rounded in profile, bear deep crural fossettes at the junction with the dental lamellae, and oblique crenulations which engage those of the sockets. Antero-lateral accessory dental socket on dorsal surface of tooth. Anterior crenulations extend over one-quarter shell length and are single ridges with pointed ends separated by deep interspaces. A median pair of crenulations reflect the distinctive median line in the costellae.

Interior of brachial valve. Adductor muscle field occupies median one-third and posterior two-thirds of valve, bounded by raised lateral margins which merge with brachio-phore bases and decrease anteriorly as they converge towards end of median ridge. Median ridge low, rounded, one-fifth width of muscle field, separates wide impressions. Brachio-phores, diverging anteriorly at about 70° , are thick, straight, erect plates, triangular in lateral profile with anterior edge normal to commissural plane, and bearing small peg-like projections which articulate with the crural fossettes (see Pl. 96, fig. 4d). Deep, triangular sockets, supported by socket pads or fulcral plates lie partially beneath

EXPLANATION OF PLATE 91

- Figs. 1–4. *Dedzietina macrostomoides*, Ashgillian of Bohemia, Kralodvorské bridlice Karlik. 1a, b, internal mould of pedicle valve USNM 165876, and rubber impression of mould, $\times 3$. 2a, b, internal mould of brachial valve USNM 165877, and rubber impression of mould, $\times 3$. 3a, b, external mould of brachial valve USNM 165878, and rubber impression of mould, $\times 3$. 4a, b, internal mould of brachial valve USNM 165879, and rubber impression of mould, $\times 3$.
- Fig. 5. *Resserella elegantula* (Dalman), Gotland. 5a–e, brachial valve, pedicle valve, anterior, posterior and side views $\times 2$, of whole shell, number Br. 1202201 of Swedish Museum of Natural History, Stockholm, here designated the lectotype.
- Fig. 6. *Resserella concavoconvexa* (Twenhofel), Jupiter Formation (late Llandoveryan) of Est River Anticosti Island, locality F-26-ER, collected by E. Roche 1939. 6a–e, side, posterior, anterior, brachial valve and pedicle valve, of whole shell USNM 165880, $\times 4$.
- Figs. 7–10. *Resserella basalis* (Dalman), Visby Marl (late Llandoveryan C₆ to early Wenlockian), Gotland, specimens loaned by Swedish Natural History Museum, Stockholm. 7a, b, interior and anterior views of pedicle valve, $\times 2$. 8, interior view of brachial valve, $\times 2$. 9, interior view of brachial valve, $\times 2$. 10a, b, interior and posterior views of brachial valve, $\times 2$.
- Figs. 11, 12. *Resserella brownspontensis* (Amsden), late Wenlockian mudstone, old quarry about one-third of mile south-east of Golden Grove Park, about 2 miles south-west of Llandeilo, Britain, grid reference SN 601696. 11a–d, internal mould of brachial valve USNM 165881, and rubber impression and external mould of same valve and rubber impression, $\times 3$. 12a–d, external mould of brachial valve USNM 165882 and rubber impression and internal mould of same valve and rubber impression, $\times 3$.



the interarea. Concentric crenulations on the socket floor mark progressive growth stages which in older specimens produce a fulcral plate and slight lateral cavity beneath. Cardinal process with short, thick shaft and bifid myophore, on which a median groove persists on to posterior face which bears chevron-shaped crenulations. In some shells, median half of each myophore lobe projects slightly further posteriorly so that together these projections simulate a middle member of a trifold myophore. Crenulations of the valve margin as in pedicle valve.

Type specimens. No holotype was designated for *R. elegantula*. Dalman used Hisinger's collections and several specimens from Djupvik (Mulde Marl) with labels written by Hisinger, are regarded at the Swedish Museum of Natural History as syntypes. From these, specimen no. SMNH Br. 1202201, a whole shell, is here selected as lectotype (see Pl. 91, figs. 5a–e).

Distribution. Known only from the Mulde Marl (late Wenlockian) of Gotland. Locality, Old Brickyard, 3.3 km south-west of Klinte, Gotland. Map reference, CJ 313606. The species appears to be very localized. References to *R. elegantula* from other areas where checked, are found to be misidentifications.

Remarks. Neither Dalman nor Lindström recognized the presence in Gotland of the species named in 1839 as *O. canalis* J. de C. Sowerby, nor have subsequent authors. Consequently resserellinids from Gotland, other than *V. visbyensis* and *R. basalis* have been taken to be *R. elegantula* (Dalman). Unfortunately Dalman's figures (1828, pl. II, figs. 6a–b), which show only external views, give the impression of a somewhat elongate form and it is understandable that later authors, having only these figures would be likely to apply the name *R. elegantula* to the elongate Wenlockian–Ludlovian resserellid—which in fact is *R. canalis*. Thus Davidson in 1847 (p. 62), 1848 (p. 321), and 1869 (p. 211) (see synonymy) assigned to '*O.*' *elegantula*, British Wenlockian forms which are certainly not conspecific with the true *R. elegantula* from the Mulde Marl. Without interior views we cannot be certain of all, but most of the specimens figured by Davidson are clearly of *R. canalis* (J. de C. Sowerby) which Davidson put into synonymy with '*Dalmanella*' *elegantula* Dalman, no doubt under the impression (from Dalman's figures) that *elegantula* was an elongate form. Many subsequent misidentifications stemmed from this decision of Davidson.

A measure of the unreliability of Dalman's figure (1828, pl. II, fig. 6) is the fact that the outline appears to be distinctly triangular—especially the anterior half. In fact, it appears as if more sharply triangular than the outline of *R. basalis* given in the same plate (pl. II, fig. 5). *R. basalis* which can be clearly recognized on other criteria (see later) is the resserellid with the most triangular anterior outline and Dalman's plate II, fig. 6, is a misleading representation of *R. elegantula*.

Resserella basalis (Dalman)

Plate 91, figs. 7a, b, 8, 9, 10a, b; Plate 98, figs. 7a–f; Plate 99, figs. 2a–e, 3a–e, 4a–e, 5, 6a, b;
Plate 100, figs. 3a, b, 5a–e

1828 *Orthis basalis* Dalman, p. 116, pl. II, figs. 5a–e.

1837 *Orthis basalis* Hisinger, pl. 20, figs. 12a, b.

non 1838 *Orthis basalis* von Buch, p. 60, pl. 2, fig. 9.

non 1869 *Orthis basalis* Dalman (?); Davidson, p. 217, pl. XXVII, figs. 10–11.

- non 1912 *Orthis (Dalmanella) basalis* Dalman; Reed, p. 22, pl. 9, figs. 6-9.
 non 1917 *Orthis (Dalmanella) basalis*, Dalman; Reed, p. 849, pl. IX, fig. 7.
 1932 *Parmorthis basalis* (Dalman); Schuchert and Cooper, p. 129.
 non 1934 *Parmorthis basalis* (Dalman); Lamont, fig. 11.
 non 1952 *Dalmanella basalis* (Dalman 1827); sensu Lindström, Dahmer, p. 90, pl. II, figs. 19-21.
 non 1956 *Parmorthis basalis* (Dalman); Curtis, p. 150.

Diagnosis. Ventribiconvex *Resserella* with distinctly triangular anterior outline and beaks widely separated. Bifurcation of the median costellae in the brachial valve is completed relatively early so that the medial costellae in the anterior region are sub-parallel.

Comparison. *R. basalis* is distinguished from *R. elegantula* by its more triangular outline, flatter brachial valve, longer, less incurved interarea of the pedicle valve, much smaller teeth, thinner dental lamellae, thinner, more curved brachiophores, different cardinal process, and relatively shorter muscle field in the brachial valve. *R. basalis* is close to *R. waldronensis*, especially in the arrangement of medial costellae in the brachial valve. However, *R. basalis* has a more triangular outline and greater separation of the beaks.

R. concavoconvexa also has widely separated beaks but the pedicle valve beak is more incurved, crossing the commissural plane and the dorsal interarea is erect (i.e. normal to the commissural plane) whereas in *R. basalis* it is anacline. Moreover these two species may be distinguished by the relative convexity of the valves, the brachial valve of *R. concavoconvexa* becoming concave anteriorly.

R. elegantuloides also shows a high apsacline ventral interarea and wide separation of the beaks but is easily distinguished by its distinctive ribbing.

Description. Exterior. Ventribiconvex, convexity decreasing antero-laterally. Brachial valve only slightly convex posteriorly, with shallow median sulcus widening anteriorly. Outline sub-triangular to shield-shaped. Length equal to width and twice the thickness. Hinge line straight, long, about five-sevenths of greatest width which is at one-third shell length. Cardinal angles slightly rounded. Anterior commissure crenulate and sulcate, lateral commissures gently flexed. Pedicle valve projects one-fifth total length posterior to hinge line with gently curved beak not overhanging hinge line. Brachial valve beak slightly incurved. Beaks widely separated by a distance equal to one-fifth of maximum length. Ventral interarea one-quarter long as wide, gently curved, apsacline, lateral margins sharp. Dorsal interarea half length of ventral interarea, anacline slightly curved apically. Delthyrium open, triangular enclosing about 30°. Notothyrium open, partially occupied by myophore which does not extend into delthyrium. Costellae 3 per mm at 5 mm length, about 45 on 9 mm wide shell. Branching pattern in median area of brachial valve asymmetrical, with few relatively early bifurcations.

Interior of pedicle valve. Muscle field short and wide, almost confined to delthyrial cavity. Median ridge absent. Laterally inclined dental lamellae support small triangular teeth. Lateral cavities, deep and conical, penetrate beneath interarea. Teeth bear crural fossettes elongate normal to commissural plane.

Interior of brachial valve. Adductor muscle field confined to median third of posterior half of valve. In some specimens muscle field slightly elevated with raised margins. Median ridge broad and low, extends to mid-length and separates weak impressions, anterior pair of which are separated from larger posterior pair by transverse ridges normal to median ridge. Postero-laterally directed ridges connect median ridge to brachiophore

bases (see Pl. 91, figs. 8–10). Brachiophores, diverging anteriorly about 50°, are triangular with anterior edge normal to commissural plane. Small sockets are supported on socket pads or fuleral plates. Cardinal process with triangular bilobed myophore. Crenulations of anterior margin low, rounded and separated by rounded interspaces.

Type specimens. No holotype was designated for '*O.*' *basalis*. Dalman, however, used Hisinger's collection from Klinteberg, Gotland, and from this material in the Swedish Museum of Natural History, Stockholm, specimen no. Br. 2298, the original of Dalman's pl. II, figs. 5a–e, is here selected as lectotype. It is refigured on our Plate 100, figs. 5a–e.

Distribution. *R. basalis* is known from the Visby Marl (late Llandoveryian C₆ to early Wenlockian) and the Högkint Group (Wenlockian), of Gotland. Also from the Wenlock Limestone of the Welsh Borderland.

Localities. Wenlock Limestone (middle nodular member), west side of Wren's Nest Hill, Dudley, Staffordshire, grid reference SO 935921; Wenlock Limestone, quarry opening on Ledbury–Malvern road, one-third of a mile east of Ledbury, grid reference SO 378716; Wenlock Limestone, old quarry at Iron Bridge in Benthall Wood, grid reference SJ 665034; Shales immediately above the Wenlock Limestone (?Wenlockian—see Walmsley, 1959, p. 487), old limestone workings south of the road from Monkswood to Glascoed, Usk inlier, Monmouthshire, grid reference SO 333016.

The range is thus Wenlockian—possibly extending into late Llandoveryian.

Remarks. Of the known *Resserella* species occurring earlier than *R. basalis*, *R. concavoconvexa* seems to be the closest and is possibly ancestral. The specimens figured by Davidson 1869 (pl. XXVII, figs. 10 and 11), from Falfield, near Tortworth and referred by him to '*Orthis basalis* Dalman (according to Lindström)', is not *R. basalis* Dalman and appears to be a new species now being described by Dr. M. G. Bassett. This is the species referred to by Curtis (1956), and may possibly be the species referred to by Reed (1912 and 1917) and Lamont (1934)—see synonymy.

Resserella concavoconvexa (Twenhofel)

Plate 91, fig. 6a–e, Plate 100, fig. 6a–e

1927 *Dalmanella concavoconvexa* Twenhofel, p. 179, pl. XVI, figs. 1–3.

1963 *Resserella concavoconvexa* (Twenhofel, 1927); Rubel, p. 134, pl. V, figs. 1–7.

Diagnosis. (Tentative only, because no internal material available.) Transversely shield-shaped *Resserella*, ventribiconvex posteriorly, brachial valve becoming concave anteriorly (i.e. resupinate). Beaks well separated, dorsal interarea normal to commissural plane (catacline), ventral interarea incurved apsacline. Anterior commissure broadly sulcate, lateral commissures curved.

Comparison. *R. concavoconvexa* is similar to *R. elegantula* in outline but is distinguished by its resupinate brachial valve, catacline dorsal interarea, and greater extension of the pedicle valve beak posterior to the hinge line. From *R. canalis* it is distinguished by its greater relative width and its resupinate brachial valve. In its well separated beaks it resembles *R. basalis* but differs in the attitudes of the interareas as well as its rounded anterior margin.

Description. As no material showing internal features of this species has been available, no complete description can be given.

Types. The holotype, figured by Twenhofel 1927 (pl. XVI, figs. 1-3), is YPM 10339 of the Peabody Museum of Natural History, Yale University. It is refigured in our Plate 100, figs. 6a-e.

Distribution. *R. concavoconvexa* is recorded by Twenhofel (1927, p. 179) from the Jupiter Formation (late Llandoveryan, C₃-C₆) of Anticosti Island. *R. cf. concavoconvexa* was recorded by Boucot, Johnson, Harper, and Walmsley 1966 (p. 13, pl. III, figs. 15-17, 21-25), from unnamed beds (late Llandoveryan C₄-C₅), Back Bay, New Brunswick, GSC locality 55050. *R. cf. concavoconvexa* has been noted in a collection made by Ollerenshaw (1961), from the Matepedia Valley, Quebec, (Loc. nos. NCO 571, Jan. 34-37), of late Llandoveryan, C₃-C₅ age. Rubel 1963 (p. 134, pl. V, figs. 1-7), recorded *R. concavoconvexa* from Estonia and on p. 137 gave the range of this species in Estonia as Jaani and Jaagarahu stages. According to Rubel (1963, p. 110), these horizons are Wenlockian. On p. 138 Rubel records *R. visbyensis* from the same horizons. On Gotland *Visbyella visbyensis* is known from the Visby Marl (late Llandoveryan C₆-earliest Wenlockian). *R. cf. concavoconvexa* occurs, poorly preserved, in material collected by Walmsley from two localities in South Wales. From mudstone (late Llandoveryan, C₄) at the south end of the rock face, close to the stream junction at Mandinam, Llandovery district, grid reference SN 742282 and from Canaston Beds (late Llandoveryan, ?C₅-C₆), south bank of Eastern Cleddau River, about 5 miles east of Haverfordwest, Pembrokeshire, grid reference SN 048139. The range of *R. concavoconvexa* is thus late Llandoveryan (C₃-C₆) to possibly early Wenlockian and from Anticosti, ?New Brunswick, ?Quebec, ?South Wales, and Estonia.

Resserella waldronensis (Foerste)

Plate 93, figs. 2a-e, 3a-d, 4a, b, 5a, b

1879 *Orthis elegantula* Dalman; Hall, p. 150, pl. 21, figs. 11-17, *non* Dalman.

1917 *Dalmanella waldronensis* Foerste, p. 245.

Diagnosis. Plano-convex to slightly biconvex *Resserella* with sub circular outline. Medium coarse costellae, sub-parallel in medial region of brachial valve where bifurcation is complete relatively early. Pedicle valve, only slightly (one-tenth) longer than brachial valve, interareas meet at an angle of less than 90°. Margins of delthyrium subtend almost 90°.

Comparison. *R. waldronensis* resembles *R. basalis* in the arrangement of medial costellae of the brachial valve but is distinguished by its much smaller but more incurved beak of the pedicle valve, which results in closer proximity of the beaks. In *R. basalis* the pedicle valve also projects considerably further posteriorly beyond the hinge line. In outline and relative biconvexity, *R. waldronensis* resembles *R. brownsportensis* but the latter has a distinctive, finely costellate median depression along the pedicle valve and a medial triangular panel of finer costellae on the brachial valve. Moreover, in *R. brownsportensis* the dorsal muscle field extends into the anterior half of the valve and is bounded by a strong margin whereas in *R. waldronensis* it barely extends to mid-length and lacks a well-developed margin. In *R. brownsportensis* the beak of the pedicle valve projects further posterior to the hinge line and the angle subtended by the margins of the delthyrium is less than in *R. waldronensis*.

Description. Exterior. Ventribiconvex, almost plano-convex, brachial valve slightly convex posteriorly with shallow median sulcus widening anteriorly so that valve becomes almost plane. Outline sub-circular, commonly somewhat triangular anteriorly. Length equal to width and two and a half times the thickness. Hinge line straight equals two-thirds maximum width which is near mid-length. Cardinal angles slightly rounded, anterior commissure crenulate and broadly sulcate. Lateral commissure slightly flexed. Pedicle valve projects only one-tenth total length posterior to hinge line, with barely incurved beak. Interareas meet at less than 90° . Ventral interarea curved, apsacline, one-fifth as long as wide, lateral margins sharp. Dorsal interarea two-thirds length of ventral interarea, plane anacline. Delthyrium and notothyrium both open and triangular enclosing about 90° . Notothyrium filled by protruding myophore. Costellae 3 per mm at 5 mm length, about 60 costellae on 9 mm wide shell.

Interior of pedicle valve. Floor of delthyrial cavity concave, smooth, lacking median ridge or impressed muscle tracks. Dental lamellae erect, not extended forward of teeth. Teeth small, blunt, triangular, with distinct accessory sockets. Crural fossettes at junction with dental lamellae. Lateral cavities small. Crenulations of anterior margin low, rounded, separated by narrow interspaces.

Interior of brachial valve. Adductor muscle field occupies median one-third and posterior two-fifths of valve. Median ridge, broad, low, one-quarter width of muscle field, narrows sharply anteriorly. Posterior impressions strong and bounded by raised lateral margins which merge into brachio-phore bases. Anterior impressions weak. Brachio-phores diverging anteriorly about 60° are erect, triangular plates, thickened distally but terminating in fine points. Socket pads support wide, triangular crenulated sockets. Cardinal process with broad, commonly carinate shaft and bifid myophore with crenulated posterior face protruding beyond notothyrium.

Type specimens. The specimens figured by Hall 1879 (p. 150, pl. 21, figs. 11–17), bearing catalogue number 1765/3, in the American Museum of Natural History, New York.

Distribution. *R. waldronensis* occurs in the Waldron Shale (Wenlockian) of Indiana.

Localities. Paps Crossing and Vail Quarry, Sandusky, Indiana.

Resserella elegantulina (Davidson)

Plate 99, figs. 7a–c; Plate 100, figs. 1a–e, 2a–c

1881 *Orthis elegantulina* Davidson, p. 152, pl. V, fig. 12.

1883 *Orthis elegantulina* Davidson; Davidson, p. 219, pl. XIII, fig. 17.

Diagnosis. Relatively small, thick-shelled, ventribiconvex, dorsally sulcate *Resserella* with sub-circular outline and costellae which are moderately coarse and even. Anterior commissure deeply sulcate.

Comparison. In its outline and broadly sulcate anterior commissure, *R. elegantulina* resembles *R. concavoconvexa*, but is distinguished by its small size, relatively coarser ribbing and its anacline dorsal interarea. From *R. canalis*, *R. elegantulina* is distinguished by its more transverse outline, more convex brachial valve and its coarser and more even

costellae in the medial areas of both valves. In *R. canalis* both the medial depression of the pedicle valve and the narrow triangular medial panel of the brachial valve are occupied by finer costellae. *R. elegantulina* has a relatively shorter hinge line and more rounded cardinal angles than has *R. canalis*.

Description. Small, thick-shelled, ventribiconvex. Sulcus of brachial valve widens anteriorly. Outline transversely sub-elliptical to sub-circular. Length almost equal to width and one and a half times thickness. Hinge line straight equals two-thirds width. Cardinal angles rounded. Anterior commissure crenulate and strongly unisulcate, lateral commissures flexed. Pedicle valve projects one-ninth total length beyond hinge line, beak commonly incurved. Ventral interarea curved apsacline with sharp lateral margins, dorsal interarea plane, anacline. Delthyrium triangular enclosing about 65°. Costellae broadly rounded, even, 3 per mm at 5 mm length.

Interior of pedicle valve. Floor of delthyrial cavity smooth, lacking median ridge. Dental lamellae erect, anterior edges normal to commissural plane. Teeth bluntly triangular in plan and profile, bear crural fossettes and accessory sockets.

Interior of brachial valve. Adductor muscle field elevated on a platform reaching almost to anterior margin along median one-third of valve. Medial ridge one-third width of muscle field, extends two-thirds length. Brachiophores, stubby distally, fuse with socket pads to form deep triangular sockets. Bifid cardinal process protrudes from notothyrium. Anterior crenulations strong and medially fuse with anterior edge of muscle platform.

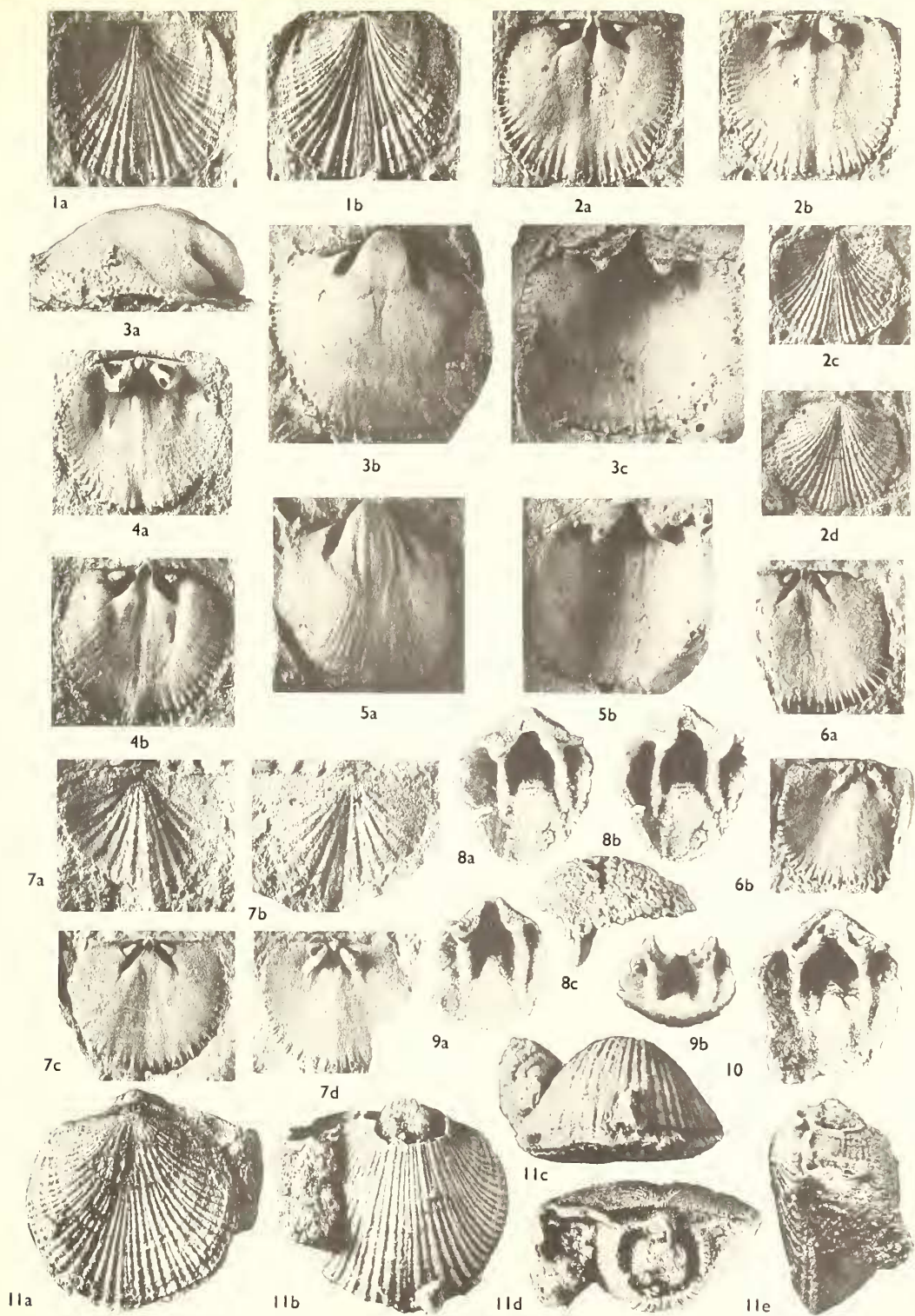
Type specimens. The type lot of *R. elegantulina* consisted of 85 whole shells all registered in the British Museum (Natural History) under one number B.5649. From these a lectotype has been selected and re-registered as BB.32232. Its dimensions are length 5.3 mm,

EXPLANATION OF PLATE 92

Figs. 1–5. *Resserella brownsportensis* (Amsden), late Wenlockian mudstone, old quarry about one-third of mile south-east of Golden Grove Park, about 2 miles south-west of Llandeilo, Britain, grid reference SN 601696. 1a, b, external mould of brachial valve USNM 165883, and rubber impression, $\times 3$. 2a–d, internal mould of brachial valve USNM 165884, and rubber impression and external mould of same valve and rubber impression, $\times 3$. 3a–c, lateral and ventral views of internal mould of pedicle valve USNM 165885 and rubber impression, $\times 3$. 4a, b, rubber impression and internal mould of brachial valve USNM 165886, $\times 3$. 5a, b, internal mould of pedicle valve USNM 165887 and rubber impression, $\times 3$.

Figs. 6, 7. *Resserella sefinensis* sp. nov., late Llandoveryan (C₁), about 50 ft east of rock step on east side of small stream entering River Sefin ('Afon Bran' of Ordnance Map), about 30 ft from the junction of the two streams, about 2 miles east of Llangadock, Britain, grid reference SN 742282. 6a, b, internal mould of brachial valve USNM 165888, and rubber impression, $\times 4$. 7a–d, external mould of brachial valve USNM 165889 (here designated holotype), and rubber impression and internal mould of same valve and rubber impression, $\times 4$.

Figs. 8–11. *Resserella logansportensis* sp. nov., Kenneth Limestone (Pridolian), USNM locality 12347, abandoned quarry at Kenneth Station, about 5 miles west of the centre of Logansport, Indiana. 8a–c, interior of pedicle valve USNM 165890, oblique view of interior and lateral view to show teeth, $\times 5$. 9a, b, interior and anterior views of pedicle valve USNM 165891, $\times 5$. 10, interior view of pedicle valve USNM 165892, $\times 5$. 11a–e, brachial valve, pedicle valve, anterior, posterior, and lateral views of USNM 165893, $\times 4$, here designated holotype.



width 5.7 mm, and thickness 2.9 mm. Its locality was Loc. 29 of Davidson and Maw 1881, from the Buildwas Beds, early Wenlockian of Shropshire.

Distribution. *R. elegantulina* occurs in the Buildwas Beds (early Wenlockian) of Shropshire, Britain.

Locality. North bank of River Severn, about 400 yd south-east of Buildwas, Shropshire, grid reference SJ 639046.

Remarks. *R. elegantulina* appears about the same time as *R. basalis* and it is possible that both were derived from *R. concavoconvexa*. These three species and *R. waldronensis* have similar ribbing patterns by which they may be distinguished from other *Resserella* species.

Resserella logansportensis sp. nov.

Plate 92, figs. 8a-c, 9a, b, 10, 11a-e; Plate 93, figs. 1a-e

Diagnosis. Elongate, plano-convex to slightly biconvex weakly sulcate *Resserella* with moderately coarse even costellae. Median ridge of pedicle valve wide, flat, and raised. Dental lamellae erect, teeth long and curved. No interiors of brachial valves were available.

Comparison. *R. logansportensis* is closest to *R. canalis* in its elongate outline and ribbing pattern, but is even more elongate and has a more convex brachial valve.

The interiors of the pedicle valves are easily distinguished. In *R. canalis* the dental lamellae are widely divergent and the median ridge is not raised, whereas in *R. logansportensis* the dental lamellae are erect and the median ridge is distinctly raised.

Description. Exterior. Small. Ventribiconvex to almost plano-convex with shallow median sulcus widening anteriorly on brachial valve. Outline elongately elliptical. Length one-third greater than width and twice the thickness. Pedicle valve projects one-fifth maximum length posterior to hinge line with incurved beak overhanging hinge line. Hinge line straight, two-thirds maximum width which is near mid-length. Cardinal angles slightly rounded, anterior margin pointed. Anterior commissure crenulate and gently sulcate, lateral commissures gently flexed. Ventral interarea, curved apsacline, lateral margins rounded. Dorsal interarea one-third length of ventral interarea, plane, anacline. Both notothyrium and delthyrium open and triangular. Latter enclosing about 60°, notothyrium occupied by protruding myophore. Costellae 4 per mm at 5 mm length, about 50 on 9 mm wide shell.

Interior of pedicle valve. Narrow, deeply impressed diductor tracks are separated by a broad, low, slightly rounded median ridge which increases in height to mid-length where it ends in broad gentle anterior slope. Vertical walls of delthyrial cavity extend forward as thick, erect dental lamellae supporting long, curved, pointed teeth, tips of which project posterior to hinge line. Crural fossettes mark junction of teeth and lamellae. Lateral cavities small and deep. A pedicle callist fills apex of delthyrium.

Type specimens. Specimen USNM 165893, figured Plate 92, fig. 11a-e, is designated holotype. Specimens USNM 165890-165892 figured Plate 92, figs. 8-10 are paratypes.

Distribution. *R. logansportensis* occurs in the Kenneth Limestone (Pridolian age),

Logansport, Indiana. USNM locality 12347, abandoned quarry at Kenneth Station about 5 miles west of the centre of Logansport, Indiana.

Remarks. The material from the Kenneth Limestone is silicified and two whole shells and about twenty pedicle valves were available. Although no interiors of brachial valves have yet been seen, it is clear that this is a distinct species of *Resserella*—possibly derived from *R. canalis*.

Resserella amsdeni sp. nov.

Plate 93, fig. 6a-e; Plate 94, figs. 1a-d, 2a-e, 3, 4a-e

Diagnosis. Transversely shield-shaped, plano-convex to slightly biconvex *Resserella* with a raised median area in the dorsal sulcus and a deep median depression along the arch of the pedicle valve. The ribbing is finely fascicostellate.

Comparison. *R. amsdeni* is distinguished from all other species of *Resserella* by its deep median depression of the pedicle valve and opposing raised medial area in the dorsal sulcus. The slightly fascicostellate ornament is seen also in *R. elegantuloides*, but these species are easily distinguished by the high pedicle valve interarea of *R. elegantuloides* which also lacks the distinctive medial areas of *R. amsdeni*. *R. brownspontensis* has a slight median depression in the pedicle valve but does not have a raised medial area in the dorsal sulcus and is readily distinguished from *R. amsdeni* by its non-fascicostellate ornament.

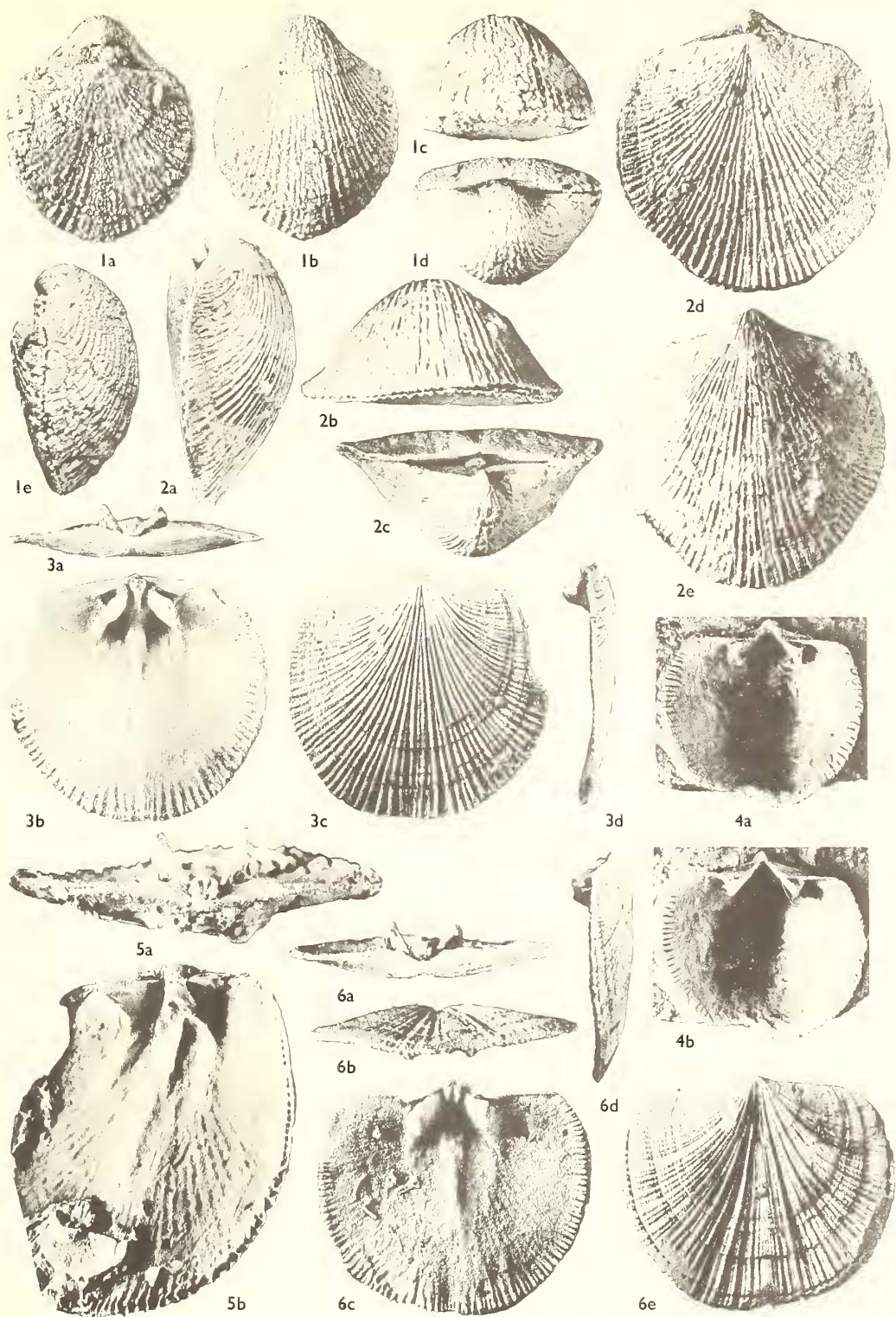
Description. Exterior. Plano-convex to slightly biconvex, convexity decreasing antero-laterally. Median triangular sulcus extending to anterior margin of brachial valve, encloses a triangular median raised area. Pedicle valve has a complementary median depression. Outline transversely shield-shaped, width greater than length, thickness equals two-fifths of length. Cardinal angles gently rounded. Beak of pedicle valve projects one-sixth maximum length posterior to hinge line which it does not overhang. Anterior commissure weakly bisulcate and crenulate, lateral commissures straight. Hinge line straight, equals three-quarters of maximum width, which is near mid-length. Ventral interareas one-tenth as long as wide, concave apsacline, dorsal interarea half as long as ventral interarea, plane anacline. Both notothyrium and delthyrium open, triangular, enclosing 100° and 90° respectively. Notothyrium filled by protruding myophore. Ornament semi-fascicostellate, fine costellae, 5 per mm at 5 mm length, even finer along median areas of each valve, about 80 on 9 mm wide shell.

EXPLANATION OF PLATE 93

Fig. 1. *Resserella logansportensis* sp. nov., Kenneth Limestone (Pridolian), USNM locality 12347, abandoned quarry at Kenneth Station, about 5 miles west of the centre of Logansport, Indiana. 1a-e, brachial valve, pedicle valve, anterior, posterior and lateral views of USNM 165894, $\times 4$.

Figs. 2-5. *Resserella waldronensis* (Foerste), Waldron Shale (Wenlockian) of south-east Indiana. 2a-e, lateral, anterior, posterior, brachial valve and pedicle valve of USNM 165895, $\times 3$. 3a-d, posterior, internal, external, and lateral views of brachial valve USNM 165896, $\times 3$. 4a, b, anterior and interior views of specimen USNM 165897, $\times 3$. 5a, b, posterior and oblique interior views of brachial valve USNM 165898, $\times 4$.

Fig. 6. *Resserella amsdeni* sp. nov., Henryhouse Formation (Ludlovian) locality Amsden 1958, P4, small quarry south-east side of road, SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3 T. 2N, R.6E, Pontotoc County, Oklahoma. 6a-e, posterior, anterior, interior, lateral, and external views of brachial valve USNM 165899, $\times 4$.



Interior of pedicle valve. Muscle field very faintly impressed, confined to delthyrial cavity in which median area only faintly raised. Dental lamellae very short, attached high on delthyrial walls, support small teeth which project beyond dental lamellae. Lateral cavities small and deep. Deep, rounded crural fossettes immediately below junction of teeth and lamellae. Teeth, triangular in plan and cross section, with bluntly rounded lateral profiles, bear antero-lateral accessory dental sockets. Anterior crenulations rounded, with median groove and separated by deep narrow interspaces, extend over one-sixth shell length.

Interior of brachial valve. Muscle field occupies median third of posterior half of valve. Median ridge, one-quarter width of muscle field extends to mid-length. Raised lateral margins fuse with brachiophore bases and anteriorly converge on median ridge. Anterior adductor impressions smaller than posterior pair, not separated by distinct ridges. Short, straight, erect brachiophores diverging anteriorly at about 70°, have sub-triangular profile with anterior edges inclined slightly posteriorly near distal extremities which bear small peg-like projections. Small sockets on low socket pads extend partially beneath interarea and have faint transverse crenulations. Cardinal process with short, broad shaft and bifid myophore with distinct median groove and crenulated posterior face.

Type specimens. Specimen USNM 165903, figured Plate 94, fig. 4a-e is designated holotype. Specimens USNM 165899 figured Plate 93, fig. 6a-e and USNM 165900-165902, figured Plate 94, figs. 1-3, are paratypes.

Distribution. *R. amsdeni* is known from the Henryhouse Formation (Ludlovian) of Oklahoma.

Localities. Amsden 1958, P4, small quarry, south-east side of road SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3 T. 2N, R. 6E, Pontotoc County, Oklahoma; Amsden 1958, P6, small glade south of road SE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 4, T. 2N, R. 6E, Pontotoc County, Oklahoma; Amsden 1958, P 7, small roadside (west) outcrop of Henryhouse, NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec 32 T. 3N, R. 6E, Pontotoc County Oklahoma.

Remarks. This species seems to be the most likely ancestor to *R. elegantuloides* and was possibly derived from *R. brownsportensis*, or directly from *R. canalis*.

Resserella brownsportensis (Amsden)

Plate 91, figs. 11a-d, 12a-d; Plate 92, figs. 1a, b, 2a-d, 3a-c, 4a, b, 5a, b; Plate 98, figs. 3a-e, 4a-d, 5a-d, 6

1860 *Orthis elegantula* Roemer (*non* Dalman), p. 62, pl. 5, fig. 7.

1949 *Parmorthis brownsportensis* Amsden, p. 42, pl. 1, figs. 1-6.

non 1951 *Parmorthis brownsportensis* Amsden; Amsden, p. 74, pl. 16, figs. 17-23.

1958 *Resserella brownsportensis* (Amsden); Amsden, p. 148.

Diagnosis. Plano-convex *Resserella* with elongate shield-shaped to sub-circular outline. Costellae broad, rounded, except in median depression of pedicle valve and median triangular panel of brachial valve where costellae are much finer.

Comparison. *R. brownsportensis* is closest to *R. canalis*, especially in outline, relative convexity of valves, interior of the pedicle valve and presence of a median depression on pedicle valve. However, in *R. brownsportensis* the lateral margins tend to be sub-parallel, the anterior margin straighter, the beak is commonly less incurved, the smaller

teeth do not project across the commissural plane, the umbo of the pedicle valve is relatively narrower and the costellae are broader and more rounded.

In its relatively coarse and broad costellae and relatively narrow umbo it is the closest species to *R. crassicostata* but the latter is distinctive in its extremely coarse ornament.

From *R. amsdeni*, *R. brownsportensis* is most easily distinguished by its more elongate outline and its more even and broader costellae as well as by its lack of the distinctive raised median area in the dorsal sulcus and the deep median depression along the pedicle valve.

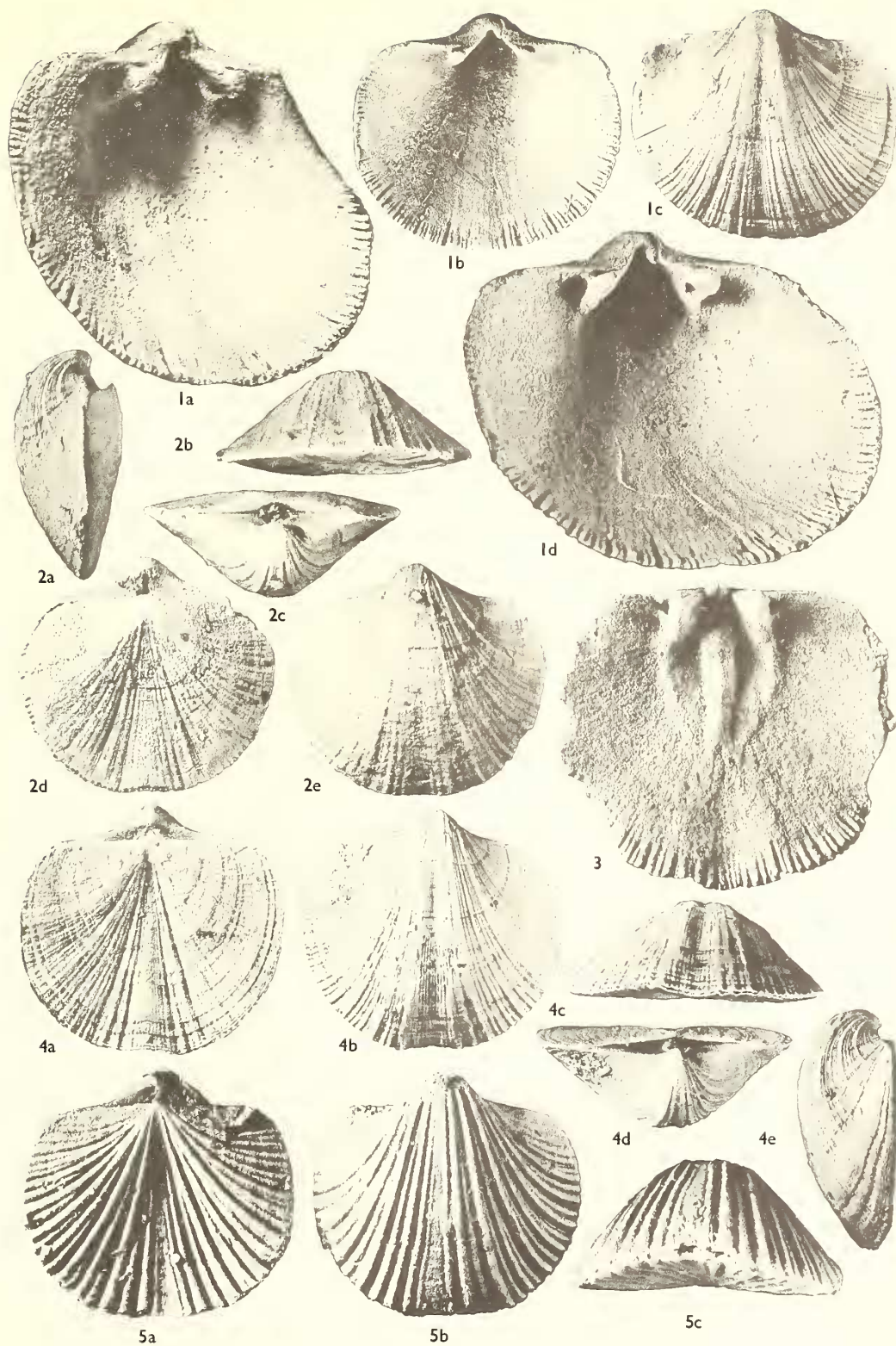
Description. Exterior. Plano-convex, pedicle valve decreasing in convexity antero-laterally and having a wide shallow median depression, brachial valve with median sulcus widening anteriorly, median portion flat. Outline elongate shield-shaped to sub-circular. Length greater than width and twice the thickness. Pedicle valve projects one-fifth total length posterior to hinge line with incurved beak overhanging hinge line. Cardinal angles barely rounded, anterior commissure crenulate and weakly unisulcate, lateral commissures slightly flexed. Hinge line straight equals two-thirds maximum width which is at mid-length. Ventral interarea curved, apsacline to orthocline, with sharp lateral margins; dorsal interarea shorter, plane, anacline. Both notothyrium and delthyrium open, triangular, latter enclosing about 45°, notothyrium filled with protruding myophore. Costellae broad, rounded, 3 per mm at 5 mm length, about 60 on 9 mm wide shell. Finer costellae in median areas.

Interior of pedicle valve. Narrow, elongate, well-impressed diductor tracks flank a broad, flat median area extending two-fifths shell length before ending in a gradual slope to mid-length. A fine median ridge probably separated adductor muscles whose track is presumably represented by the flat median area. Adjustor impressions present along lower part of delthyrial walls. Sub-parallel vascula media extend forward from diductor tracks. Wide pedicle callist present. Laterally divergent dental lamellae support small, triangular teeth with curved anterior edges, small deep crural fossettes and wide accessory sockets. Lateral cavities small and deep.

Interior of brachial valve. Large, slightly raised adductor, muscle field, half width and two-thirds length of shell. Raised margins fuse with brachiophore bases and anteriorly

EXPLANATION OF PLATE 94

- Figs. 1-4. *Resserella amsdeni* sp. nov., Henryhouse Formation (Ludlovian), Pontotoc County, Oklahoma. 1a-d, locality Amsden 1958, P4, small quarry south-east side of road, SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 3T. 2N, R. 6E. 1a, interior pedicle valve USNM 165900, $\times 5$. 1b, c, internal and external views of same valve, $\times 3$. 1d, oblique interior view of same valve showing teeth and crural fossette, $\times 5$. 2a-e, locality Amsden 1958, P6, small glade south of road, SE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 4, T.2N, R.6E, lateral, anterior, posterior, brachial valve and pedicle valve of whole specimen USNM 165901, $\times 5$. 3. locality Amsden 1958, P7, small roadside (west) outcrop, NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 32 T. 3N, R. 6E, interior of brachial valve USNM 165902, $\times 5$. 4a-e, locality Amsden 1958, P6, small glade south of road, SE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 4, T. 2N, R. 6E, brachial valve, pedicle valve, anterior, posterior and lateral views of whole shell USNM 165903, $\times 3$, here designated holotype.
- Fig. 5. *Resserella crassicostata* (Schuchert and Cooper), Henryhouse Formation (Ludlovian), locality Amsden 1958, P6, small glade south of road, SE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 4, T.2N, R. 6E. 5a-c, brachial valve, pedicle valve, and anterior views of whole shell USNM 165904, $\times 5$.



fade as they converge on median ridge which is low, rounded, quarter width of muscle field and narrows anteriorly. No transverse ridges present but posterior impressions deeper. Erect brachiophores diverge anteriorly at 70° and thicken distally becoming triangular in plan. Sockets small, crenulated, and supported on socket pads. Cardinal process has thick broad shaft and distinctly bilobed myophore with crenulated triangular posterior face. Anterior crenulations of shell margin strong, rounded, with pointed tips and separated by deep interspaces.

Type specimen. The holotype is specimen no. YPM 17510 of the Peabody Museum, Yale University. It was figured by Amsden 1949 (pl. 1, figs. 2–3). Specimen no. YPM 17512 from the same locality is refigured here, our Plate 98, fig. 5a–d.

Distribution. *R. brownsportensis* is known from the Brownsport Formation (Ludlovian), Tennessee. For details of the many localities see Amsden 1949, p. 42. Amsden 1951 recorded this species from the Henryhouse Formation (Ludlovian) of Oklahoma but the specimens figured by him (pl. 16, figs. 17–23) are more coarsely ribbed and less parallel-sided and are considered to be *R. crassicosata* (Schuchert and Cooper 1932). *R. brownsportensis* has been found in material collected by Boucot from late Wenlockian mud-stones of the Llandeilo district, South Wales.

Locality. Old quarry about one-third mile south-east of Golden Grove Park, about 2 miles south-west of Llandeilo, grid reference SN 601696.

Remarks. *R. brownsportensis* is somewhat intermediate in morphology between *R. canalis*, *R. amsdeni*, and *R. crassicosata*. It seems likely that it was derived from *R. canalis* during late Wenlockian time. *R. crassicosata* which occurs in both the Brownsport Formation and the Henryhouse Formation, of Ludlovian age, may have been derived from *R. brownsportensis* or have had an independent origin from *R. canalis* during the Wenlockian.

Resserella crassicosata (Schuchert and Cooper)

Plate 94, figs. 5a–c; Plate 95, figs. 1a–f, 2a–c, 3a, b, 4a, b, 5a–e, 6a, b, 7

1932 *Parmorthis crassicosata* Schuchert and Cooper, p. 129, pl. 21, figs. 4–5.

1951 *Parmorthis brownsportensis* Amsden; Amsden, p. 74, pl. 16, figs. 17–23, *non* Amsden 1949.

Diagnosis. Transversely shield-shaped to sub-circular plano-convex *Resserella* having relatively few and coarse sub-angular costellae, except in the median areas of both valves, where the costellae are fine.

Comparison. *R. crassicosata* is distinct amongst resserellids because of its very coarse costellae. In general shape and outline it resembles *R. amsdeni* but has distinct ornament and lacks the characteristic median fold and depression in the dorsal sulcus and pedicle valve. In its pattern of broad, strong costellae enclosing finer costellae in the median areas of both valves, it somewhat resembles *R. brownsportensis* but is distinguished by the number and coarseness of its costellae.

Description. *Exterior.* Plano-convex, brachial valve with shallow sulcus widening anteriorly, pedicle valve with finely costellate slightly depressed median area. Outline

shield-shaped to sub-circular. Length equal to width and two and a half times the thickness. Pedicle valve projects one-sixth total length posterior to hinge line, beak gently incurved, not overhanging hinge line. Cardinal angles obtuse. Anterior commissure crenulate and unisulcate, lateral commissures straight. Hinge line straight, almost three-quarters maximum width which is at mid-length. Ventral interarea curved, apsacline with rounded lateral margins. Dorsal interarea shorter, plane, anacline. Both notothyrium and delthyrium open, triangular, latter enclosing about 70°. Notothyrium filled with protruding myophore. Costellae sub-angular, coarse, 2.5 per mm at 5 mm length, finer costellae in median areas. Only about 35 costellae on 9 mm wide shell.

Interior of pedicle valve. Muscle field faintly impressed, confined to median third of posterior third of valve, barely extending beyond delthyrial cavity. Wide, short diductor tracks separated by faintly raised median area. Short, laterally divergent dental lamellae support blunt, triangular teeth which project anterior of lamellae. Deep semi-cylindrical crural fossettes at junction of teeth and lamellae.

Interior of brachial valve. Adductor muscle field extends beyond mid-length in median third of valve, bounded by raised margins which merge with brachiophore bases and anteriorly fade towards median ridge. Median ridge low, rounded, one-quarter width of muscle field, narrows anteriorly. Faint transverse ridges separate smaller anterior impressions. Short, thick, straight brachiophores, laterally and anteriorly divergent, have pointed tips, and anterior edges normal to commissural plane. Wide triangular sockets. Cardinal process with short thick shaft and bilobed myophore. Crenulations of anterior shell margin coarse, wide, rounded, with median groove and deep narrow interspaces.

Type specimen. The holotype is specimen Cat. No. 913, Schuchert Collection, Yale University, and is recorded by Schuchert and Cooper 1932, p. 129, from Martin Mills, western Tennessee.

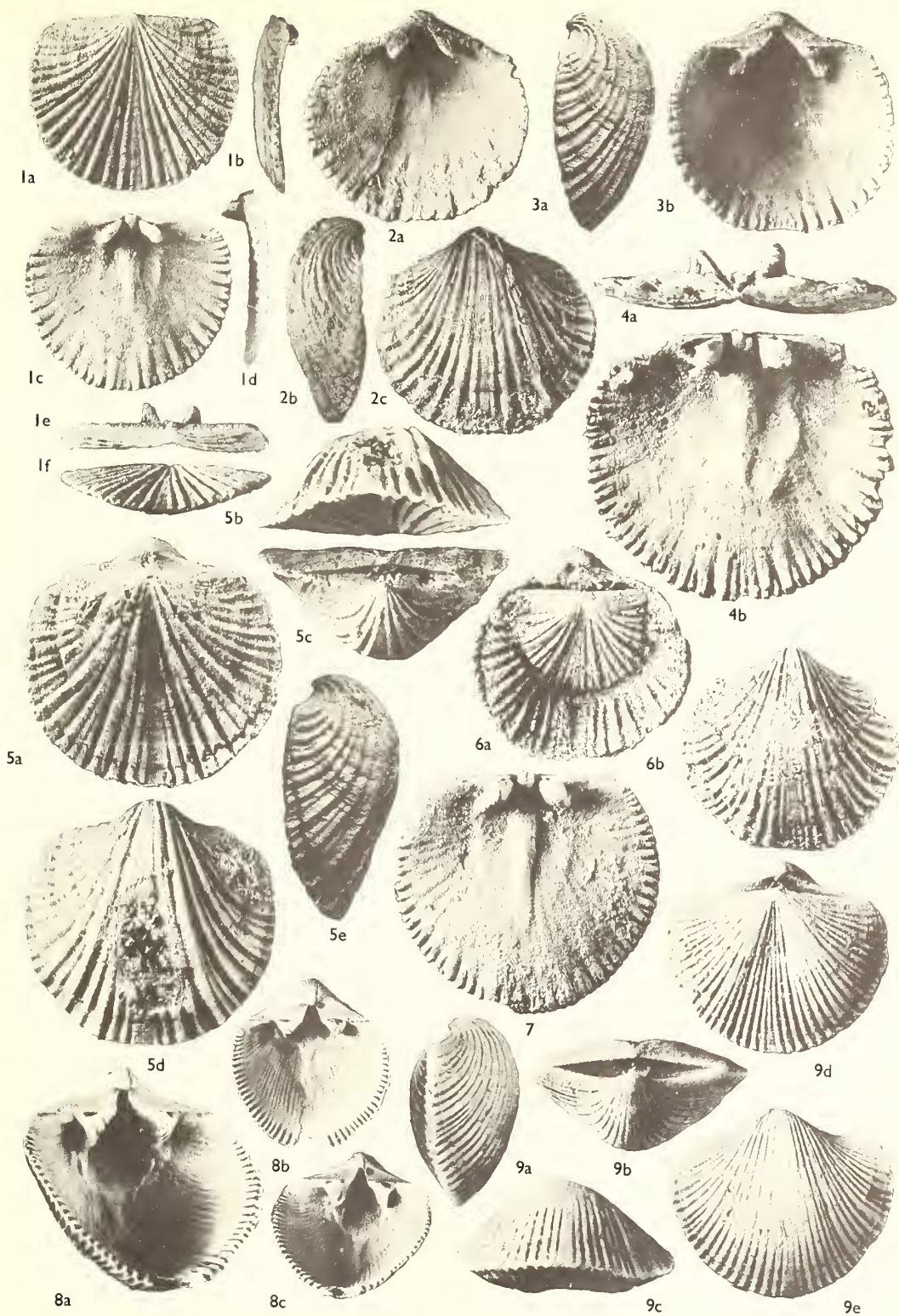
Distribution. *R. crassicostata* occurs in the Brownsport Formation (Ludlovian) of Tennessee and the Henryhouse Formation (Ludlovian) of Oklahoma.

Localities. Amsden 1951, Collection 3, Henryhouse Formation; east side of road in bluff for half a mile, NW $\frac{1}{4}$ SW $\frac{1}{4}$, sec. 4, T. 2 N, R. 6E, Pontotoc County, Oklahoma, Amsden 1951, Collection 15, Henryhouse Formation (upper); SW $\frac{1}{4}$ NW $\frac{1}{4}$, sec. 33, T. 3N, R. 6E, Pontotoc County, Oklahoma; Amsden 1951, Collection 16, Henry-

EXPLANATION OF PLATE 95

Figs. 1-7. *Resserella crassicostata* (Schuchert and Cooper). Figs. 1, 2, and 6, Brownsport Formation (Ludlovian) locality, glade 150 yd south of Mount Lebanon Community Centre, Perry County, Tennessee. Figs. 3, 4, 5, and 7, Henryhouse Formation (Ludlovian), locality Amsden 1958, P6, small glade south of road, SE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 4, T. 2N, R. 6E, Pontotoc County, Oklahoma. 1a-f, external, lateral, internal, lateral, posterior, and anterior views of brachial valve USNM 165905, $\times 4$. 2a-c, interior, lateral, and exterior views of pedicle valve USNM 165906, $\times 3$. 3a, b, 4a, b, posterior and interior views of brachial valve USNM 165907, $\times 5$. 5a-e, brachial valve, anterior, posterior, pedicle valve, and lateral views of whole shell USNM 165908, $\times 5$. 6a, b, brachial and pedicle valves of whole shell USNM 165909, $\times 3$. 7, interior of brachial valve USNM 165910, $\times 5$.

Figs. 8, 9. *Resserella elegantula* (Dalman), Mulde Marl (Wenlockian), locality old brickyard, 3.3 km south-west of Klinte, Gotland, grid reference CJ 313606. 8a, oblique view of interior of pedicle valve USNM 165911, $\times 5$, showing large crenulated teeth. 8b, c, interior and anterior views of same specimen, $\times 2$. 9a-e, lateral, posterior, anterior, brachial and pedicle valves of whole shell USNM 165912, $\times 4$.



house Formation, (upper coral beds); N $\frac{1}{2}$ SW $\frac{1}{4}$, sec. 4, T. 2N, R. 6E, Pontotoc County, Oklahoma. Amsden 1958, P. 6, Henryhouse Formation, small glade, south of road, SE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 4, T. 2N, R. 6E, Pontotoc County, Oklahoma. Brownsport Formation, glade, 150 yd south of Mount Lebanon Community Centre, Perry County, Tennessee.

Remarks. This species was first described, by Schuchert and Cooper (1932, p. 129), from the 'Niagaran' of Martin's Mills, Western Tennessee. It is considered to have diverged from early forms of *R. brownsportensis* or possibly to have arisen directly from *R. canalis*.

Resserella springfieldensis (Foerste)

Plate 101, figs. 4a-e

1917 *Dalmanella springfieldensis* Foerste, p. 245, pl. XI, figs. 5A-E.

1954 *Parmorthis elegantula* (Dalman); Nikiforova, p. 46, pl. II, figs. 1-2 (*non* Dalman).

1960 *Parmorthis* (*Parmorthis*) *elegantula* (Dalman); Sarycheva, pl. XIII, fig. 12 (*non* Dalman).

Diagnosis. *Resserella* with thick, long, anteriorly divergent dental lamellae extending almost to mid-length. Delthyrial cavity wide and smooth or with weak median ridge. Brachiophores short, thick, widely divergent. Median ridge in brachial valve almost reaches anterior margin.

Comparison. *R. springfieldensis* is distinguished from *R. sefinensis* by its shorter, thicker brachiophores, more pronounced median ridge in the brachial valve and finer costellae. From *R. canalis*, *R. springfieldensis* is distinguished by relatively longer and less divergent dental lamellae and by its wider medial panel of finer costellae in the pedicle valve, but otherwise these species are close and *R. springfieldensis* may have given rise to *R. canalis*. *R. concavoconvexa* differs from *R. springfieldensis* in its resupinate brachial valve and proportionately greater width.

Description. Exterior. Plano-convex with non-sulcate brachial valve and strongly arched pedicle valve. Outline elongately elliptical. Length greater than width and twice the thickness. Pedicle valve projects one-fifth total length posterior to hinge line with slightly incurved beak. Cardinal angles obtuse, anterior commissure crenulate and recti-marginate, lateral commissures straight. Hinge line straight, equal to four-fifths maximum width which is slightly posterior to mid-length. Ventral interarea curved, apsacline, two-fifths as long as wide, lateral margins rounded. Delthyrium triangular, open. Costellae rounded, 3 per mm at 5 mm length, finer costellae along median area of pedicle valve.

Interior of pedicle valve. Faintly impressed muscle field confined to wide, deep, smooth delthyrial cavity with only slightly elevated median area. Strong, thick dental lamellae inclined at 45° to commissural plane, project anterior to smooth triangular teeth, and extend almost to mid-length. Crural fossettes deep and curved.

Interior of brachial valve. Faintly impressed muscle field confined to median third of valve, extends into anterior half, with low rounded median ridge one-sixth width of muscle field, extending to three-quarters length. Weak lateral margins merge into brachiophore bases but fade anteriorly. No distinct transverse ridges, but anterior pair of impressions appear to be the larger. Brachiophores, short thick divergent plates. Sockets small, raised on socket pads. Cardinal process with short shaft and small compressed myophore.

Type specimens. Eleven specimens numbered 87122 are labelled as syntypes in the Smithsonian Institution, U.S. National Museum.

Distribution. *R. springfieldensis* was recorded by Foerste (1917 p. 245), from the Cedarville Dolomite (Wenlockian) of Eastern Mills Quarry, south-west of Springfield, Ohio. The specimens figured by Nikiforova (1954, pl. 11, figs. 1–2), as *Parmorthis elegantula* from the Kitaigorod Formation (late Llandoveryan C₄–C₆) of Podolia are considered to be conspecific. Material collected by Dr. A. M. Ziegler from the Woolhope Limestone (early Wenlockian) of May Hill, Welsh Borderland, and housed in the Oxford University Museum, includes a resserellid referred to '*R. cf. elegantula*'. Examination of this material by Walmsley reveals that this species is *R. springfieldensis*.

Localities. 1. Northwest of Old Oaks Farm, grid reference SO 68692244. 2. Stream section, 180 yd S. 83° W., of Hill Farm Glass house, grid reference SO 70552103.

Two poorly preserved specimens of *Resserella* collected by Dr. M. G. Bassett from the Woolhope Limestone are also considered to be conspecific with *R. springfieldensis*.

Localities. 1. Main quarry at Scutterdine, Woolhope, Herefordshire, grid reference, SO 577372. 2. Old quarry, north side of road between Alfrick and Crews Hill (Malverns area), grid reference SO 73995291.

The known distribution of the species is thus late Llandoveryan (C₄–C₆) of Podolia, early Wenlockian of the Welsh Borderland and Wenlockian of Ohio.

Remarks. *R. springfieldensis* is considered to have given rise to *R. canalis* in the Wenlockian.

Resserella elegantuloides (Kozłowski)

Plate 98, figs. 8a, b; Plate 99, figs. 1a–e

1929 *Dalmanella elegantuloides* Kozłowski, pp. 63–67, text-figs. 9A, 10, 11; pl. II, figs. 1–16.

1932 *Dalmanella* ? *crassiformis* Kozłowski; Paeckelmann and Sieverts, p. 27, pl. 1, figs. 10a–d.

1954 *Parmorthis elegantuloides* (Kozłowski); Nikiforova, pp. 48–50, pl. II, figs. 3–6.

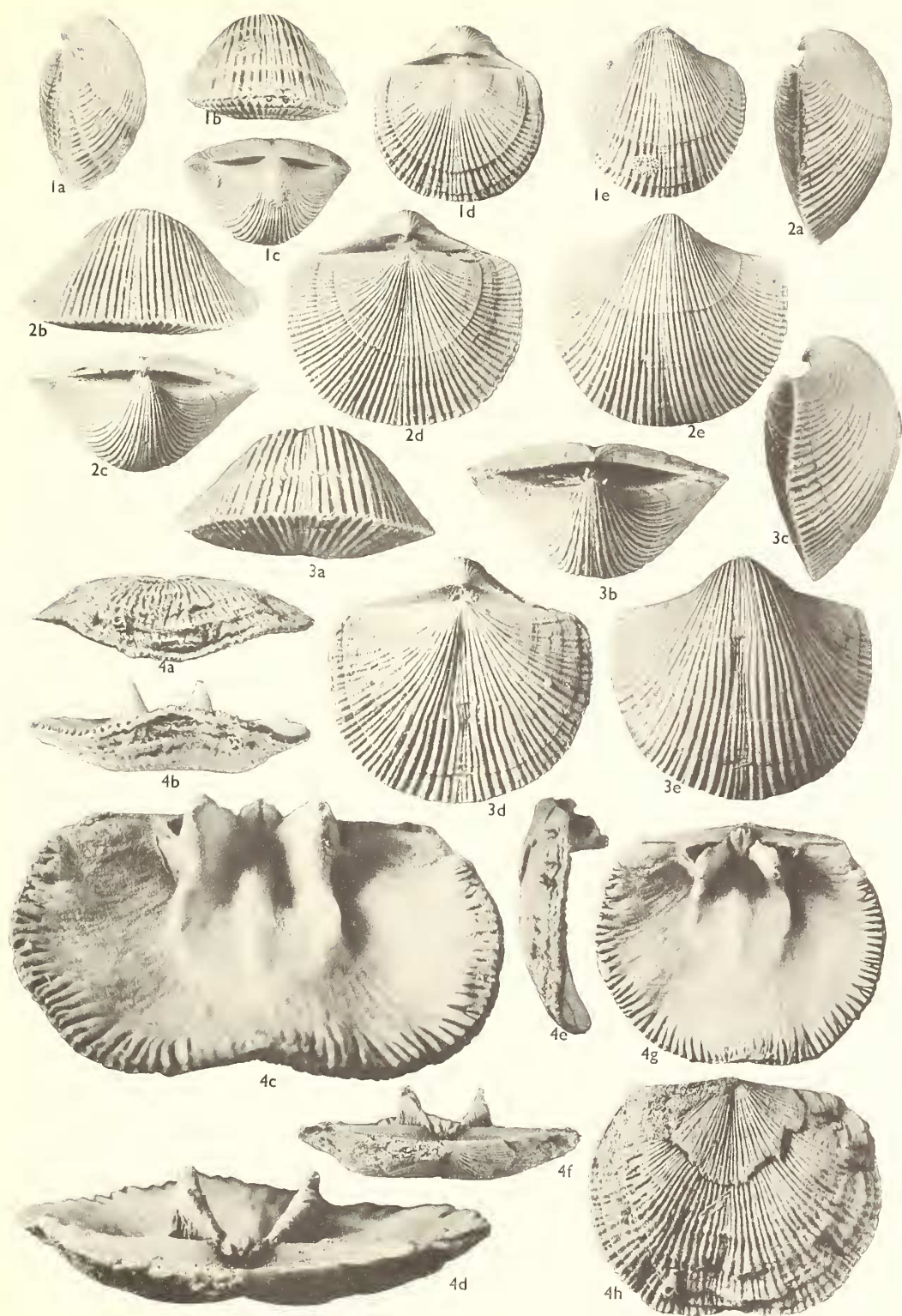
non 1963 *Resserella* aff. *elegantuloides* (Kozłowski); Kul'kov, p. 14, pl. 1, fig. 1.

Diagnosis. Ventribiconvex, dorsally sulcate *Resserella* with relatively high ventral inter-area and distinctive ornament in which 12–14 more prominent costellae are developed amongst numerous fine costellae.

Comparison. In its semi-fascicostellate pattern of ornament *R. elegantuloides* is closest to *R. amsdeni* from which it may be distinguished, however, by the absence of the latter's characteristic fold in the dorsal sulcus, and sulcus in the ventral fold. Nevertheless the slightly depressed median area of the pedicle valve of *R. elegantuloides* supports the view

EXPLANATION OF PLATE 96

Figs. 1–4. *Resserella elegantula* (Dalman) Mulde Marl (Wenlockian), locality, old brickyard, 3.3 km, south-west of Klinte, Gotland, grid reference CJ 313606. 1a–e, lateral, anterior, posterior, brachial and pedicle valves of whole shell USNM 165913, $\times 2$. 2a–e, lateral, anterior, posterior, brachial and pedicle valves of whole shell USNM 165914, $\times 3$. 3a–e, anterior, posterior, lateral, brachial, and pedicle valves of whole shell USNM 165915, $\times 4$. 4a, b, anterior and posterior views of brachial valve USNM 166535, $\times 3$. 4c, d, anterior and posterior views of same specimen $\times 5$, showing brachiophores and crenulated sockets. 4e–h, lateral, posterior, internal, and external views of same specimen, $\times 3$.



suggested by the similar style of ornament and similar high ventral interareas that these species may be fairly closely related.

Description. Exterior. Ventribiconvex with shallow median sulcus widening anteriorly on gently convex brachial valve. Outline sub-circular. Length equal to width and twice the thickness. Pedicle valve projects one-fifth of total length posterior to hinge line, beak erect, barely incurved. Beaks separated by distance equal to one-quarter length of hinge line. Cardinal angle slightly rounded. Anterior commissure crenulate and broadly unisulcate, lateral commissures straight. Hinge line straight, equals three-quarters greatest width which is near mid-length. Ventral interarea, apsacline, almost orthocline, slightly incurved at apex, three-tenths as long as wide, lateral margins sharp. Dorsal interarea half as long, plane, anacline. Notothyrium and delthyrium both open and triangular, enclosing 60° and 30° respectively. Myophore does not project from notothyrium. Costellae rounded, 3 per mm at 5 mm length, about 100 on 9 mm wide shell. About 12 costellae on pedicle valve stronger than average, producing an uneven semi-fasci-costellate aspect. Median sectors of both valves have finer sub-parallel costellae.

Interior. No material showing the interior of either valve was available. However, Kozłowski (1929, fig. 10) diagrammatically illustrated the internal features, which are clearly resserellid.

Type specimens. Kozłowski (1929, pp. 63–67) did not designate a holotype but the specimen figured by him in his pl. 2, fig. 1, which he described as ‘Echantillon typique’ is here selected, with his agreement, as lectotype.

Distribution. *R. elegantuloides* was stated by Kozłowski (1929, p. 67) to be characteristic of the Borszczów stage (Gedinnian), especially the middle part. It also occurs in the Gedinnian of Nevada (see Johnson, Boucot, and Murphy 1967, p. 684).

Remarks. *R. elegantuloides* may have been derived from *R. amsdeni*. No descendant species is known in the Siegenian, but *R. triangularis* (Emsian) has similar fine ribbing and may be derived from *R. elegantuloides*.

Resserella sefinensis sp. nov.

Plate 92, figs. 6a, b, 7a–d

Diagnosis. Small *Resserella* with plane to slightly sulcate brachial valve and relatively few broad costellae, lacking finer costellae in median sector of brachial valve. Pedicle valve not known.

Comparison. In the coarseness of its ornament *R. sefinensis* somewhat resembles *R. crassicostata* but the latter bears very fine costellae along the median areas of both valves. The absence of a distinct median panel of finer costellae also distinguishes *R. sefinensis* from *R. brownsportensis* which also has relatively thicker brachiophores.

Description. Exterior of brachial valve. Small, plane, sulcate with shield-shaped outline. Costellae relatively few and uniformly coarse. A median triangular panel may be distinguished from the lateral areas but the distinctive asymmetrical branching pattern of later resserellids is not seen. Hinge line straight, three-quarters greatest width which is posterior to mid-length. Cardinal angles obtuse. Interarea anacline.

Interior of brachial valve. Muscle field faintly impressed, not clearly delimited by raised margin or elevated on a platform. Median area slightly raised as a broad, low median ridge. Brachioophores thin, erect to postero-laterally inclined plates diverging anteriorly at 90°. Sockets, deep, conical, and crenulated. The small cardinal process is a lobed myophore arising directly from the posterior end of the median ridge without a shaft. Crenulations of the anterior shell margin broad, flat, and confined to the periphery.

Type specimens. Specimen USNM 165889, figured Plate 92, figs. 7a–d, is designated holotype. Specimen USNM 165888, figured Plate 92, fig. 6a, is a paratype.

Distribution. *R. sefinensis* is known from beds of late Llandoveryan (C₁) age from the Llandovery area Wales.

Locality. About 50 ft east of rock step, on east side of small stream entering River Sefin ('Afon Bran' of Ordnance Map), about 30 ft from the junction of the two streams, about 2 miles east of Llangadock. Grid reference SN 742282, Camarthenshire.

Remarks. This species is assigned to *Resserella* despite lack of pedicle valve material because the interior of the brachial valve is resserellid in most characters. However, the poorly impressed, undefined, and unraised muscle field is not typical of the genus. Externally, the ribbing is only resserellid in its pattern of a median triangular panel flanked by lateral areas with slightly curved costellae.

It is considered that *R. sefinensis* is a primitive *Resserella* and it is certainly the oldest species yet recognized.

It seems that it was during late Llandoveryan (C₁) time that the genus *Resserella* made its first appearance. *R. sefinensis* is thus understandably not completely typical.

Resserella triangularis (Maurer)

Plate 100, figs. 7, 8a, b; Plate 101, figs. 1–3

non 1857 *Orthis triangularis* Zeiler, p. 49, pl. 4, figs. 14–16 [= *Platyorthis*, see Harper, Boucot, and Walmsley 1969, p. 86].

1889 *Orthis triangularis* Maurer, p. 160, pl. III, figs. 8–12.

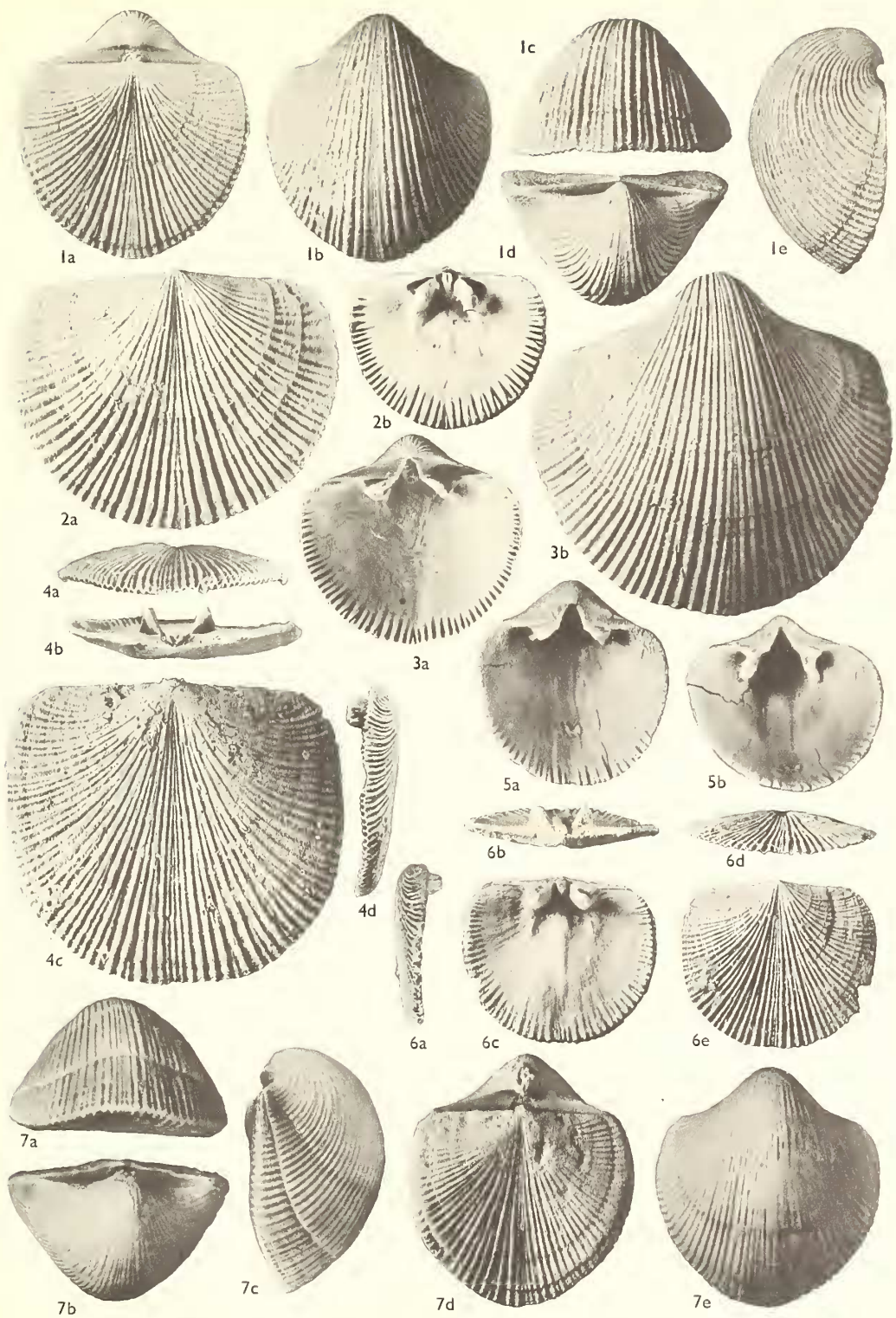
1961 *Parmorthis triangularis* (Zeiler); Kaplun, p. 67, pl. 7, figs. 8–15.

EXPLANATION OF PLATE 97

Fig. 1. *Resserella canalis* (J. de C. Sowerby), Slite Marl (Wenlockian), Gotland. 1a–e, brachial and pedicle valves, anterior, posterior and lateral views of whole shell USNM 166536, ×3.

Figs. 2, 3. *Resserella elegantula* (Dalman), Mulde Marl (Wenlockian), locality, old brickyard, 3.3 km south-west of Klinte, Gotland, grid reference CJ 313606. 2a, exterior of brachial valve USNM 166537, ×5. 2b, interior of same specimen, ×3. 3a, interior of pedicle valve USNM 166538, ×3. 3b, exterior of same valve, ×5.

Figs. 4–7. *Resserella canalis* (J. de C. Sowerby), figs. 4a–d, Slite Marl (Wenlockian), locality, canal on main road, 2 km west and slightly to south of Klinte Church, Gotland. 4a, b, anterior and posterior views of brachial valve USNM 166539, ×3. 4c, exterior of same specimen, ×5. 4d, lateral view of same specimen, ×3. 5a, b, Slite Marl (Wenlockian), locality, quarry of cement plant in Slite, Gotland, interior and anterior views of pedicle valve USNM 166540, ×3. 6a–e, 7a–e, Eke Marl (Ludlovian), locality, just north-east of main road 2 km north of Grötlingbo church, Gotland. 6a–e, lateral, posterior, interior, anterior, and exterior views of brachial valve USNM 166541, ×3. 7a–e, anterior, posterior, lateral, brachial, and pedicle valves of whole shell USNM 166542, ×3.



Diagnosis. A large *Resserella* with fine, even ribbing. Brachioophores, long, widely divergent anteriorly and posteriorly fused to prominent median ridge which extends beyond mid-length. Very narrow median ridge in pedicle valve extends from delthyrial cavity to mid-length.

Comparison. In the cardinalia and especially the long, strong brachioophores and median ridge, *R. triangularis* resembles *R. pragensis* (see Havlíček 1956, pl. X, fig. 3). However, the ribbing is quite different. *R. triangularis* has numerous fine, even ribs whereas *R. pragensis* has fewer and stronger ribs some of which are more prominent than others. In the fineness of ornament *R. triangularis* is closest to *R. elegantuloides* (see Kozłowski 1929, pl. 2, fig. 2) but the latter has semi-fascicostellate uneven ribbing, and less prominent brachioophores. *R. elegantuloides* is ventribiconvex whereas *R. triangularis* is plano-convex and much larger.

Description. Exterior. Large, plano-convex, sulcus on brachial valve widening and deepening anteriorly. Outline subcircular to shield-shaped. Length equal to width and twice the thickness. Pedicle valve projects one-fifth total length posterior to hinge line, beak barely incurved. Cardinal angles slightly rounded. Anterior commissure unisulcate and crenulate, lateral commissures straight. Hinge line straight, three-quarters of maximum width which is near mid-length. Ventral interarea apsacline, dorsal interarea anacline. Both notothyrium and delthyrium open and triangular, latter enclosing about 100°. Notothyrium filled with protruding myophore. Costellae fine, even, 3 per mm at 5 mm length, about 70 on 9 mm wide shell.

Interior of pedicle valve. Strongly impressed muscle field barely extends beyond delthyrial cavity. Slightly raised median area separates elongate adductor scars and continues to mid-length as a fine median ridge. Elongate diductor impressions extend to beginning of median ridge beyond which point parallel vascular trunks continue to mid-length. Adjustor scars on delthyrial walls extend almost to teeth. Teeth large, triangular, with large, antero-lateral crural fossettes and accessory sockets, are supported on short dental lamellae. Pedicle callist present.

Interior of brachial valve. Slightly elevated triangular muscle field with weakly defined margins extends almost two-thirds valve length and is almost half as wide as greatest width. Median ridge narrow, prominent, extends length of muscle field and posteriorly merges with notothyrial platform and shaft of cardinal process which has median groove and expanded bifid myophore. Brachioophores thick, diverging anteriorly at about 90° and inclined posterolaterally. Sockets, strongly crenulated, antero-laterally aligned, lack fulcral plates or socket pads and bear small denticles along posterior edges. Crenulations of anterior shell margin narrow, rounded, separated by slightly wider interspaces are confined to periphery.

Type and figured specimens. The material figured by Maurer 1889 (pl. III) is housed in the Hessisches Landesmuseum, Darmstadt. Specimen no. Mu. 5409 is the original of his fig. 8 and is labelled from Lahneck. Specimen no. Mu. 4568 is the original of his fig. 9 and specimen no. Mu. 4566 is the original of his figs. 10 and 10a. Specimen no. Mu. 5409 is here selected as lectotype.